PALAEOVEGETATION and ENVIRONMENT at CETHANA, TASMANIA

by

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This thesis contains no material which has been accepted for the award of any other higher degree or graduate diploma in any tertiary institution and, to the best of my knowledge and belief, it contains no material previously published or written by any other person, except when due reference is made in the text of the thesis.

R. J. Carpenter

ABSTRACT

The Oligocene (ca 35 Ma) Cethana fossil deposit in northern Tasmania is investigated, with the aim of reconstructing the vegetation and environment. Aspects of the geology, palynology and particularly the macrofossil component of the flora are considered. The flora is discussed in the context of the development of the Australasian vegetation.

The sediments are believed to have been deposited in a lake situated in a topographically diverse region. In particular, perturbations to the facies by siliceous debris suggests the lake was proximal to a steep slope. The macrofossils are represented by impressions or carbonised compressions from which fragments of cuticle can be recovered. Scanning electron microscopy is an important technique used to examine and compare fossil and extant cuticles. Pteridophyte macrofossils identified include specimens of Hymenophyllaceae, *Lygodium* (Schizaeaceae) and *Sticherus* and *Gleichenia* (Gleicheniaceae). Gymnosperm macrofossils identified are the extinct cycad *Pterostoma*, *Macrozamia* (Zamiaceae), *Acmopyle*, *Dacrycarpus*, *Dacrydium*, *Phyllocladus*, *Lagarostrobos* and *Podocarpus* (Podocarpaceae), *Agathis* and *Araucaria* (Araucariaceae) and *Libocedrus* and *Papuacedrus* (Cupressaceae). Angiosperm macrofossils have affinity to three of the four subgenera of *Nothofagus* (Fagaceae), *Gymnostoma* (Casuarinaceae), *Lomatia*, *Banksia/Dryandra* and other genera (Proteaceae), *Callicoma*, *Vesselowskya* and *Weinmannia/Cunonia* (Cunoniaceae), *Brachychiton* (Sterculiaceae), Elaeocarpaceae, Lauraceae and Myrtaceae. Detailed taxonomic descriptions are provided for some of the macrofossils.

The palynoflora is of low diversity but is overwhelmingly dominated by *Nothofagus* and gymnosperm pollen. There is a high level of taxonomic correlation between the macro- and microfloras.

Extant species with close affinity to the fossil taxa occur in many regions of the Southern Hemisphere, including New Guinea, New Caledonia, New Zealand, Tasmania and eastern Australia. Strong floristic and physiognomic similarities to the

fossils are now to be found in microthermal rainforests of these regions. The prevailing climate at Cethana in the Oligocene is therefore considered to be cool with uniformly high levels of rainfall and humidity. The co-occurence of taxa now found across a broad latitudinal range is interpreted as being related to the great variety of ecophysiological niches around the lake, which would have been created by a combination of the diverse topography and palaeolatitude of ca 60° S.

A distinct element of the flora is composed of taxa with highly sclerophyllous cuticles and/or extant affinities which are typically restricted to oligotrophic habitats. These plants include diverse Proteaceae, several conifers, *Macrozamia*, *Schizaea*, *Gleichenia*, *Drosera* and Restionaceae. The presence of these taxa at Cethana provides supportive evidence for the hypothesis that the evolution of the diverse Australian scleromorphic flora was primarily related to edaphic and not climatic factors.

The Cethana flora is compared to that of numerous other Australian Tertiary deposits.

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Kirk Johnson and Gary Davidson provided geological interpretations, and Mike Macphail and Steve Forsyth helped me with palynology. Various herbaria co-operated by providing plant specimens. David Christophel and David Greenwood partly sponsored a Queensland field trip for me.

Lastly, I thank David Pemberton, Rosemary Gales, Peter Naughton and other friends for out of hours encouragement.

"I was capable of much; but I have been injured and blighted and crushed by things beyond my control!"

Eustacia Vye,
in *'The Return of the Native'*
(Thomas Hardy, 1878)

CONTENTS

CHAPTER 1

INTRODUCTION

The aim of this study is to reconstruct the vegetation and environment surrounding a single Tasmanian Tertiary fossil deposit, Cethana, using evidence drawn from as many sources as possible. Previous work on the Cethana flora resulted in the description of species of *Nothofagus* (Fagaceae) (Hill 1984), *Lomatia* (Proteaceae) (Carpenter and Hill 1988) and *Tmesipteris* (Psilotaceae) (Carpenter 1988) and a general conclusion that the climate was most suitable for microthermal vegetation (e.g. Hill and Gibson 1986a). However, apart from a relatively brief resumé of the flora in these papers, no general treatise of the deposit has been attempted.

Studies of Australian Tertiary macrofossil deposits were initiated in the 19th century by researchers such as von Ettingshausen, Deane, Johnston and von Mueller. A particularly well illustrated flora is that of Vegetable Creek in northern New South Wales (Ettingshausen 1888). This work is of significance since it was published in monograph form where the author attempted to discuss the relationships of the whole flora. In the first part of the 20th century, Chapman published several palaeobotanical papers and later, Cookson and co-workers described particularly well preserved specimens from the Victorian brown coal fields (e.g. Cookson and Duigan 1951; Cookson and Pike 1954). This work was important because the authors based their determinations on cuticular analysis. Duigan (1966) reviewed the state of knowledge of one of these sites, the Oligocene Yallourn deposit, and based on the sixteen taxa (wood, male and female cones, pollen, seeds, leaves) that she believed had been satisfactorily identified, concluded that the *Nothofagus* forests of montane New Guinea represented the most similar modern flora. However, it is significant that she noted elements in the flora which have modern equivalents now restricted to high latitude environments. She also sought to interpret the climate at the time of deposition by considering the climatic requirements of the modern taxa. This study is therefore notable because it can be seen as a combined vegetation and climate reconstruction, based on previous sound taxonomic work. However, it took no account of physiognomic and taphonomic aspects of the fossil deposit.

Clearly, the accuracy of estimating palaeoclimate from a floristic study will be greatest if all of the fossils in the deposit can be identified correctly, and if the ecological tolerances of the living relatives are well understood. Of course, this will be rarely, if ever possible. In most studies of Australian Tertiary macrofloras only a small percentage of the macrofossils present at each site have been identified. This has resulted in only limited understanding of vegetation relationships. Nevertheless, as summarised by Christophel (1989) and Hill (1990a) important recent advances have been made in the understanding of the development of aspects of the Australasian vegetation. Hill (1982) presented a parataxonomic study of the Eocene Nerriga flora of New South Wales, and later (1986) showed that most of these parataxa could be assigned to the Lauraceae, although they were of indeterminable modern generic affinity. Hill and Macphail (1983, 1985) reconstructed vegetation types and environments of Oligocene and Plio-Pleistocene floras respectively from Tasmania, based principally on macro-microfossil taxonomic evidence, although very few of the macrofossils were formally described. Similarly, relatively few macrofossil taxa have been identified and described from the Eocene Anglesea deposit of Victoria and the apparent complexity of the sedimentary environment (Christophel *et al.* 1987) makes interpretation of the whole flora difficult.

A floristic method also offers interesting biogeographic data, since the living taxa may be found remote from the region of the fossil deposit. Further, it may pose testable ecophysiological problems concerning how taxa which are now widely separated were able to co-exist in the past. In addition, if enough fossil floras are studied in detail, evidence of foliar evolutionary change in response to environmental change may be detectable. Therefore, in this study of the Cethana flora emphasis is placed on macrofossil taxonomy. However, the philosophy pursued here is that the techniques available to palaeobotanists for interpreting past floras should not be considered in isolation. For instance, apart from estimating past climates by assessing the climatic range of nearest living relatives, use can be made of foliar physiognomy (e.g. Wolfe 1990), a technique independent of taxonomic procedure. Its rationale is that the leaf morphology of living species is highly sensitive to the prevailing climate,

and presumably the same was true in the past. The regional climates surrounding the Eocene Anglesea, Golden Grove and Maslin Bay deposits of south-eastern Australia have been estimated by comparing the cumulative frequencies of fossil leaf lengths or 'foliar physiognomic signatures' to those of extant rainforest types (see Christophel and Greenwood 1989). This represents a modified form of physiognomic analysis.

Independent abiotic evidence relating to the nature of the depositional site and its physical setting both locally and regionally should also be considered, as these will affect such factors as climate, soils, aspect and drainage, and in turn the plant communities and the taphonomy of their foliar and reproductive organs. Therefore, aspects of the floristic and physiognomic make-up of the macrofossil assemblage should be considered, along with the palynoflora, the geology of the depositional site and an overview of the palaeogeographic setting. Clearly, this combined approach can provide the most balanced perspective of the overall palaeoenvironment.

The broad aims of this study inherently impose the limitation that not all aspects can be treated in great detail. Nevertheless, most speculation is based on established evidence from other fields of botanical research, and from the developing picture of the nature of the Australian Tertiary vegetation.

CHAPTER 2

LOCAL AND REGIONAL SETTING OF THE FOSSIL DEPOSIT

2.1 GEOLOGY OF THE DEPOSITIONAL SITE

The siltstone deposit in which plant fossils were found outcrops in a road cutting approximately 0.5 km above and east of the Cethana Dam, Tasmania (41° 32' S, 146° 07' E) (Hill 1984). Fig. 1d. The sedimentary rock which was collected originally is a creamy yellow to light brown-grey laminated siltstone with alternations of thin sand layers. A low energy depositional site such as a deep lake centre with fluctuating stream inflow at the margins was inferred from this. The sediments could not be accurately aged stratigraphically since they overly marine quartzose Moina Sandstone of Late Cambrian-Early Ordovician age (Bamford and Green 1988) and themselves are only overlain by recently weathered material. On subsequent field trips a further sedimentary exposure was located about 50 m to the north, separated from the original site by faulted Moina sandstone.

Currently the Cethana Dam impounds the deeply incised Forth River, the bed of the damsite being at 125 m above sea level. Apparently the situation was similar during the Tertiary when an ancestral river, the 'Lorinna Lead', and a series of lakes occurred in the valley (Spry 1958). River gravels and lacustrine sediments have been found down to about 75 m above the present river level (Paterson 1969). It is likely that the Tertiary lake systems were caused by faulting downstream of the current damsite, or possibly by basalt flow (Rawlings 1969; Paterson 1969). The Tertiary relief in the Forth area was considered by these authors to be of the order of 300 m a.s.l. with deeply incised valleys separated by interfluves whose surfaces showed prominent though not rugged topography. The topography is similar today.

Independent field observations of the Cethana site by Dr G. Davidson (University of Tasmania) and Dr K. Johnson (Denver Museum of Natural History, Colorado) support these interpretations and have led to a more detailed understanding of the nature of the depositional site. The following is a summary of Dr Johnson's report.

Field description. The fossil-bearing lake sediments consist predominantly

of fine-grained, laminated shale, mudstone and lignite. However, located within them are numerous clasts of quartzite ranging from sand size up to boulders of several metres in diameter (Fig. 1a). As stated, the lake beds occur as two distinct inliers within the basement quartzite (quartzose Moina sandstone). The exposure of the northern inlier is approximately 20-25 m long and 4-5 m high. Its northern contact with the quartzose material appears to be unconformable and sedimentary near the top of the exposure and a fault contact near its base. The former is expressed by a basal conglomerate in the lake beds and the latter by fault-derived slickensides. The slickensides indicate that the lake beds moved down relative to the quartzite. This inlier contains the majority of the quartzite clasts and the bedding is extensively deformed around the larger ones. The southern inlier is separated by 55 m of faulted quartzose Moina sandstone that occurs as a broad anticline. The lake beds of this inlier are finely laminated and in places lignitic and appear to lie disconformably on conglomeritic quartzite. Where there is contact with quartzite, the bedding drapes gently over irregularities of its surface. These drapes most likely have resulted from post-depositional compaction of lake bed sediments that were deposited directly on the quartzite surface. No clasts were observed in these sediments. The southern contact is obscured by weathering and slumping. A diagram illustrating the geology of the depositional site as outlined above is presented in Fig. 1b.

Interpretation. The absence of sand beds and ripples in the lake beds indicates that the water was deep enough for the sediments to be deposited below wave base. This varies with the size of the waves and the extent of the water body but the lake must have been more than several metres deep.

The presence of quartzite clasts in the northern inlier but apparently not the southern indicates that these boulders were derived from a cliff/talus slope to the north. The quartzite between the inliers may have actually acted as a barrier preventing this coarse material reaching the southern inlier. This scenario assumes that post-depositional faulting did not give rise to the two inliers. There is evidence of some faulting but it is considered more likely to be local and therefore the exposed outcrop approximates the shape of the original depositional basin. It is possible that this

Figure 1.

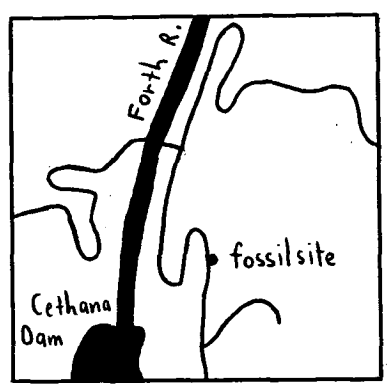
a. Cross section of a sample of fossiliferous sediment from Cethana showing pieces of angular quartzite (arrowed at top right) and black organic matter (lower centre left) distributed throughout the mudstone. Scale: 10 mm.

b. Field diagram of the Cethana road cutting showing the geology of the depositional site.

O= quartzose Ordovician material (Moina Sandstone hatched; conglomerate dotted); Q= Quaternary and recent weathered material; T= fossiliferous Tertiary sediment. The cut region in the centre is 5 m (horizontal) of Moina Sandstone. approximate Scale: 10 m horizontal; 3 m vertical. (Diagram based on a sketch and interpretations of Dr K. Johnson).

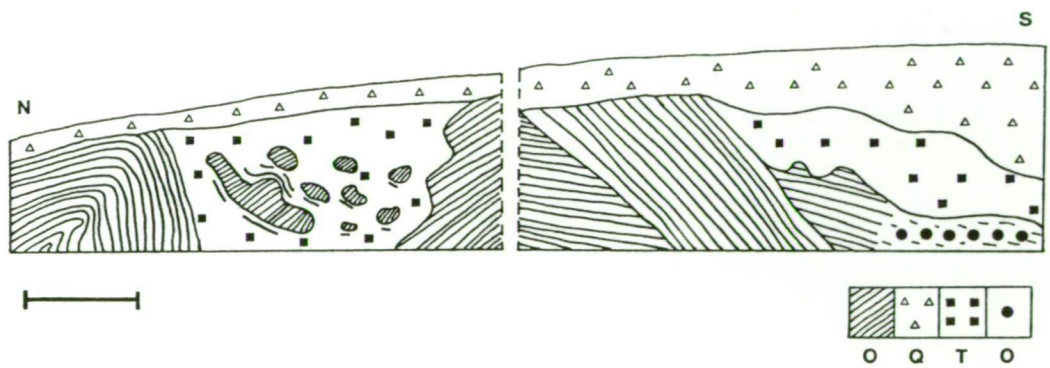
c. A reconstruction of the palaeoenvironment as proposed by Dr Johnson.

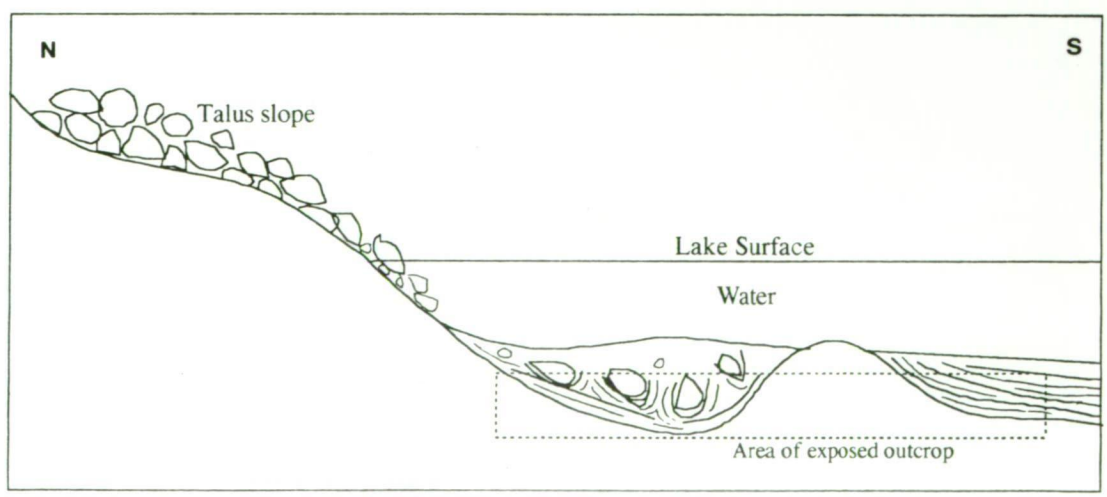
d. Location of fossil site (see Bamford and Green 1988).



a

b


S
N
Q
T
O


N
S
Talus slope
Lake Surface
Water
Area of exposed outcrop

c

quartzite formed an island in the lake rather than merely bottom topography.

The chaotic nature of the lake bed sediments surrounding the larger quartzite boulders in the northern inlier suggests some syndepositional slumping as would be expected during the implacement of large boulders in water-logged sub-aqueous soft sediment. The absence of clasts in the southern inlier indicates that it is unlikely ice-rafting was a factor. A reconstruction of the lake and environs based on geological evidence is presented in Fig. 1c.

Thin-section analysis. Dr G. Davidson also examined hand specimens and thin sections of sediments from the northern inlier. These were semi-consolidated, moderately fissile, uniform, pink to dark brown clay-shales containing abundant leaf fossils and other organic debris. Two thin sections of silty claystone were examined and consist of four principle components outlined as follows;

a) a matrix of fine smectite clays (>55 %), probably illite, given the faint greenish tinge observed in plane polarised light.

b) organic matter (>20 %), encompassing abundant fine red-brown translucent material (durain) and opaque coarse lenses and wedges representing macrofossils including leaves, stems and fruits.

c) >10 % evenly distributed silt-sized (0.02- 0.15 mm) muscovite and quartz. These are well sorted but moderately angular, consisting mainly of metamorphic quartz with sutured boundaries, elongate sub-grain development, undulose extinction, fracturing and abundant microlites. Two less abundant types are vein quartz, showing uniform extinction and vacuole trails, and possible granite derived quartz. Accessory grain types are tourmaline and plagioclase. Occasional partially eroded overgrowths occur on minor rounded grains. The even distribution of grains suggests that component c) is the result of 'steady state' accumulation.

d) lenses and clumps of terrigenous, angular silt to gravel-sized grains (>5 %) which show no gradation with the rest of the rock. Distorted wisping and bulging lenses exhibit local scouring of underlying shale, and possible cavity filling (shrinkage cracks in shale). Internally the beds are chaotic, matrix supported breccias in which no alignment of grain axes with surrounding bedding planes is apparent. Quartz

overgrowths on angular grains, and optically continuous plates of quartz amid the matrix are symptomatic of diagenetic authigenic growth. Component d) therefore consists of small scale debris deposited under a much higher flow regime than material in a)-c). No sign is evident of subsequent reworking, corroborating emplacement in a quiet sedimentary environment.

In summary the analysis indicates that steady state sedimentation deposited fine-grained carbonaceous detritus, coarse organic material such as leaves and a rain of silt. Grain sparsity and angularity imply a close to moderately close source of silt. The abundance of fine-grained carbon suggests a nearby source for this also, possibly swampy land. Coarse gravels and boulders have come from very close by, a matter of tens to hundreds of metres, and represent material shed from cliffs or slopes and emplaced as debris flows. Very fine sediments with alternations of thin sand layers imply variable stream inflow on the lake margins.

Vegetative material could thus conceivably have been deposited in a lake some 300 m a.s.l. from;

a) an adjacent swamp community,

b) vegetation surrounding the lake margins and along inflowing streams,

c) plants occuring to an unknown height above the lake, as cliff or ridge dwellers.

The vegetation surrounding the fossil deposit today occurs in edaphic conditions probably very similar to that which occurred at the time of deposition. In particular, the Cambrian-Ordovician siliceous bedrock would have resulted in oligotrophic substrates, especially on slopes, ridges and disturbed areas where build-up of organic matter and nutrient enrichment would have been limited. Conditions of high precipitation would also have had a strong leaching effect on soils.

The unusual nature of the depositional site is considered to be critical to the ecological interpretation of the fossil flora, as will be discussed later.

2.2 EARLY TERTIARY PALAEOGEOGRAPHY AND PALAEOCLIMATOLOGY OF AUSTRALASIA

Numerous reviews have been made of Late Cretaceous and Tertiary plate tectonic and associated palaeoclimatological changes in the Australasian region as they pertain to floral history, including those of Raven and Axelrod (1972), Kemp (1978, 1981), Barlow (1981) and Hill (1990a). The following is a brief summary of events in the region, based on these papers, references cited therein, and reasoned conclusions.

In the mid-Cretaceous, Tasmania and New Zealand were in close proximity in Gondwana (Lawver and Scotese 1987), and a dispersal route between these land masses and South America occurred via West Antarctica. New Caledonia lay along the eastern margin of Australia/New Guinea. With the opening of the Tasman Sea to near present proportions by the Early Eocene (55-57 million years ago [Ma]) New Zealand became an isolated land mass. At the northern apex of the Tasman Sea Australia and New Caledonia/Fiji may last have had land connection through the Queensland Plateau and the Lord Howe Rise at approximately this time (Coleman 1980; Crook 1981). Continuous land from New Zealand to New Caledonia via Norfolk Island is also considered to have been present into the Eocene. The geological evolution of the south-western Pacific is complex but it is also known that around this time an Outer Melanesian Arc began to develop and now comprises a chain of islands from northern New Guinea and the Solomons to Vanuatu, Fiji and Tonga (Colley and Hindle 1984).

At the start of the Tertiary Australia was joined to Antarctica on a broad front but during the Early Eocene (about 55 Ma) the Australian craton began moving into lower latitudes. At around this time latitudinal climatic gradients were negligible and oceans were quite uniformly warm, so that the climate at this time was the most mesic of the Cenozoic. By the end of the Eocene the northward drift and the opening of a seaway from west to east had left Australia (Tasmania) connected to Antarctica (Victoria Land) via the South Tasman Rise. The presence of land or shallow seas had effectively blocked the development of a circumpolar current. However, Tasmania was probably fully exposed to westerly polar systems, and any elevated regions prone to cool, wet

and cloudy conditions. Indeed, this expanse of water would have allowed higher and more extensive precipitation on the Antarctic continent, and contributed to ice build-up. Coldness would have been most limiting for plant growth during the long and dark winters experienced at ca 60° S and exacerbated in topographically shaded regions. The nature and timing of the uplift of the Tasmanian and eastern Australian highlands is therefore of obvious relevance to climate in the Eocene-Oligocene. In south-eastern Australia and Tasmania there is ample evidence for tectonic uplift before the Eocene and in any case most occurred before the mid-Cainozoic (Wellman 1987).

Conclusions drawn from deep sea drilling project oxygen isotope data indicate that a gradual high latitude cooling occurred throughout the Eocene followed by a marked climatic deterioration around the Eocene-Oligocene boundary, associated with decreased latitudinal heat transfer due to the initiation of a circumpolar current (Shackleton and Kennett 1975; Kennett and von der Borch 1986). The development of a deep water circumpolar current because of the final separations of Australia and South America from Antarctica resulted in the coldest south-western Pacific oceanic temperatures of the Palaeogene being recorded in the middle of the Oligocene (Kennett and von der Borch 1986). Antarctic ice cover probably built up during the Eocene and Barrett *et al.* (1987) have found evidence of sea level glacier ice on the Antarctic continent back to at least 29 Ma. In Tasmania conditions were probably colder than anywhere else in Australia, though it is not known what effect this had on the amount and distribution of rainfall, or whether snow and frost were evident. It is likely that precipitation would have decreased at this time (Truswell and Harris 1982). Nix (1982) has modelled probable climatic conditions for Australia during the Tertiary and concluded that from the mid-Eocene onwards environments suitable for microthermal vegetation have existed in Tasmania. For much of the continent, however, global cooling at this time was offset because of Australia's drift toward the Equator, and some regions of north-eastern Queensland are considered to have retained a high proportion of primitive plant groups in part because of a long and continuous period of equable climate (Webb *et al.* 1986).

Another factor associated with the plate movements that may have had an

influence on the regional and indeed global climate around the Eocene-Oligocene boundary was widespread major volcanism (Kennett *et al.* 1985). It is possible that a 'nuclear winter' effect resulted, causing a marked climatic deterioration and mass extinctions. Meteorite impacts have also been implicated (e.g. Ganapathy 1982) though it would appear that the evidence for extraordinary tectonism is sufficient to explain the observed faunal and floral extinctions (Moses 1989).

At the end of the Oligocene the build-up of polar ice and drift of the northern edge of the Australian plate into tropical latitudes resulted in increasing aridity and more marked latitudinal climatic zones. Aridity began to increase in northern Australia by about 13 Ma at least and expanded to the south during the Late Miocene (Stein and Robert 1986).

CHAPTER 3

PALYNOLOGY

3.1 INTRODUCTION

Palynological research has contributed much to an understanding of the nature of the Australian vegetation through the Tertiary. Numerous reviews have been made (e.g. Kemp 1978; Martin 1982; Sluiter and Kershaw 1982; Kershaw 1988) and a broad summary of vegetation change during the Tertiary as indicated by the pollen record is as follows. Palaeocene floras contain abundant conifer and Proteaceae pollen but *Nothofagus* is rare, Early to Middle Eocene floras were highly diverse and had numerous taxa which have affinity to modern mesothermal rainforest elements such as *Anacolosa* (Olacaceae) and Cupanieae (Sapindaceae), Late Eocene to Miocene floras are comparatively depauperate but include a preponderance of *Nothofagus* and gymnosperms, and Late Oligocene-Miocene to recent sequences indicate a rainforest decline and show a marked increase in sclerophyll woodland and herbaceous elements such as *Acacia* (Mimosaceae) Poaceae, Compositae and *Eucalyptus* (Myrtaceae). This has been associated with the appearance and development of widespread aridity.

The long sequence of sediments in the Gippsland Basin studied by Stover and Partridge (1973) has provided a stratigraphic reference for the dating of isolated deposits in the south-eastern Australian region. However, it is unreasonable to expect that the regional vegetation was uniform, and clearly the reliability of using this sequence must decrease with distance from the source. In this respect much new data has recently been accumulated from the adjacent Murray Basin (e.g. Martin 1984; Truswell *et al.* 1985; Macphail and Truswell 1989). While there is general concordance with the Gippsland and Otway Basin (Harris 1971) sequences, differences do exist.

The record of pollen and spores not only provides a broad-scale indication of vegetation change through time but has demonstrated that even after the mid-Miocene collision of the Australian and Asian plates there has been little incursion of Malesian rainforest taxa into Australia. The Australian flora is thus seen as being largely inherited from Gondwana with numerous autochthonous elements (Truswell *et al.*

1987). There is still much potential in further elucidating the nature of the Tertiary flora since there are apparently numerous taxa which have not yet been described (Truswell *et al.* 1987; Macphail and Truswell 1989). This appears to reflect the fact that the emphasis of much palynological research is geological and not botanical.

The palynological record has two major limitations for detailed interpretation of vegetation, particularly at the community level. The first is that the pollen and spores in a lake deposit such as Cethana may have been dispersed over great distances from their source, and the second is that the affinities of only a few taxa can be determined accurately to the generic level or beyond. Thus it is an aim of this study to concentrate on the macrofossil assemblage, but to complement this data with an assessment of the palynoflora.

3.2 METHODS AND MATERIALS

Pollen and spore slides were prepared from several sediment samples using standard preparation techniques by LAOLA Pty Ltd- Palynological and Micropalaeontological Sample Preparation, 95 Milne St., Bayswater, W. A. 6053. Taxa were identified with assistance from M. K. Macphail (Consultant Palynologist) and S. M. Forsyth (Mines Department, Tasmania). A sample of pollen and spores was also viewed using a scanning electron microscope (SEM), and some taxa photographed to supplement light micrographs.

3.3 AGE OF THE CETHANA DEPOSIT

A list of taxa and their proportions recorded from a sample examined by Macphail is given in table 3.1 as follows, along with different taxa found in other samples.

Table 3.1. List of Cethana pollen taxa and their modern affinities. Proportions are given for taxa identified in a sample examined by Macphail (personal communication).

taxon	% occurrence + = <1%	modern affinity
Spores		
Cyatheacidites annulatus Cookson ex Potonie		*Lophosoria quadripinnata* (Gmel.) C. Chr. (Lophosoriaceae)
Cyathidites australis Couper		Cyatheaceae
C. paleospora Martin		"
Dictyophyllidites arcuatus Pocknall & Mildenhall		Gleicheniaceae
Foveotriletes balteus Partridge		?
Gleicheniidites circinidites (Cookson) Dettmann		Gleicheniaceae
cf *Ischyosporites irregularis*		unknown pteridophyte
Laevigatosporites ovatus Wilson &Webster	1	Blechnaceae
Latrobosporites crassus Harris		? *Lycopodium* (Lycopodiaceae)
Peromonolites vellosus Stover & Partridge		Blechnaceae
Polypodiidites sp.		*Microsorium* (Polypodiaceae)
Retitriletes australoclavatidites (Cookson) Döring, Krutzsch, Mai & Schulz		*Lycopodium* cf *scariosum* Forst. f.
Trilete spore spp.	+	unknown pteridophytes
Triletes tuberculiformis Cookson		"
Verrucatosporites attinatus n. var.		monolete fern
Gymnosperms		
Araucariacites australis Cookson		Araucariaceae
Dacrycarpites australiensis Cookson & Pike	+	*Dacrycarpus* (Podocarpaceae)
Lygistepollenites florinii (Cookson & Pike) Stover & Evans	10	*Dacrydium* s. l. (Podocarpaceae)
Microcachyridites antarcticus Cookson	1	*Microcachrys tetragona* (Hook.) Hook. f. (Podocarpaceae)
Phyllocladidites mawsonii Cookson ex Couper	5	*Lagarostrobos franklinii* (Hook. f.) (Podocarpaceae)
Podocarpidites ostentatus		Podocarpaceae
P. spp.	10	"
Podosporites parvisaccites s. l.	1	*Microcachrys*?
P. microsaccatus Dettmann	2	*Phyllocladus* (Podocarpaceae)
Angiosperms		
Droseraceae		*Drosera* (Droseraceae)
Ericipites crassiexinus Harris		Ericaceae/Epacridaceae
E. scabratus Harris		"
Granodiporites nebulosus Stover & Partridge		*Embothrium coccineum* Forst. (Proteaceae)
Haloragacidites harrisii (Couper) Harris		Casuarinaceae
Liliacidites sp.		Liliaceae
Malvacipollis duratus n. sp.		Euphorbiaceae
M. subtilis Stover		"
Milfordia hypolaenoides Erdtman		Restionaceae
Nothofagidites asperus (Cookson) Stover & Evans	9	*Nothofagus menziesii* group
N. deminutus (Cookson) Stover & Evans		extinct *Nothofagus* form
N. emarcidus (Cookson) Harris/*heterus* (Cookson) Stover & Evans	53	*Nothofagus brassii* group
N. falcatus (Cookson(Stover & Evans		"
N. flemingii (Couper) Potonie	7	*N. fusca* group
N. goniatus (Cookson) Stover & Evans		*N. brassii* group
Periporopollenites demarcatus Stover	+	Trimeniaceae ?
P. polyoratus (Couper) Stover	+	Caryophyllaceae ?
P. vesicus Stover	+	"

Proteacidites spp.	+	Proteaceae
cf *P. pseudomoides* Stover		"
Tricolpites spp.	+	numerous angiosperms
T. reticulatus Cookson		*Gunnera* (Gunneraceae)
Tricolporites spp.		numerous angiosperms

Other taxa identified, including those by S. M. Forsyth

Spores	
Cyathidites minor Couper	Cyatheaceae
Foveotriletes palaequetrus Partridge	?
Herkosporites elliotii Stover	?
Lycopodiumsporites sp.	*Lycopodium*
Matonisporites ornamentalis (Cookson) Partridge	*Dicksonia* (Dicksoniaceae)
Stereisporites sp.	*Sphagnum* (Sphagnaceae)
Verrucosisporites aff. *cristatus* Stover & Partridge	?
Gymnosperms	
Cycadopites sp.	Cycadales
Angiosperms	
Gothanipollis bassensis Stover & Partridge	Loranthaceae
Myrtaceidites parvus Cookson & Pike	non-eucalypt Myrtaceae
M. mesonesus Cookson & Pike	"
Nothofagidites cf *brachyspinulosus* (Cookson) Harris	*Nothofagus fusca* type
Proteacidites reticulatus Cookson	Proteaceae
Quintinia psilatispora Martin	*Quintinia* (Escalloniaceae)
Tricolporites cf *angurium* Partridge	?

According to M. K. Macphail (personal communication), the possible age of the Cethana sediments based on the palynoflora ranges from the *Proteacidites tuberculatus* Zone (Oligocene) of Stover and Partridge (1973) into the Miocene. The maximum age is based on the presence of *Cyatheacidites annulatus* and *Verrucatosporites attinatus* n. var. and the minimum age is based on the high frequency of *Nothofagidites flemingii* (7 %). S. M. Forsyth (personal communication) has also identified *Gothanipollis bassensis* and considers that the presence of this taxon and the relatively high proportion of *Periporopollenites vesicus* tends to restrain the age of the deposit to the Lower to Middle *P. tuberculatus* Zone, which corresponds to the Early Oligocene (about 35 Ma). These palynologists also note that there is little possibility of being able to significantly refine this range since Tasmanian sediments of this age are typically depauperate in known indicator taxa. The overall diversity of pollen and spore species in the Cethana sediments is low, but the proportions of species varied slightly. For instance, most samples had more Casuarinaceae than the sample examined by Macphail (up to 8 %) and one sample had 9 % Proteaceae species. However, there was no evidence for a temporal stratigraphic sequence. Rather,

variation is probably due to differential input from different vegetation types or random concentrated input via reproductive structures. Many of the sediment samples examined yielded no pollen and spores, and the preservation of grains in others was poor. Several species are illustrated in Figs 2 and 3.

3.4 PALAEOVEGETATION SUGGESTED BY THE PALYNOFLORA

Cethana is typical of Oligocene floras of south-eastern Australia in that *Nothofagidites* species and gymnosperms overwhelmingly dominate the palynoflora (e.g. Tulip *et al.* 1982; Macphail and Truswell 1989). Apart from *Nothofagidites* species with no extant morphological affinity (e.g. *N. deminutus*), *Nothofagus* species which produce pollen very similar to the fossil taxa now occur across the latitudinal range of the genus (Dettmann *et al.* 1990). Pollen of the type now produced exclusively by species in New Guinea and New Caledonia (subgenus *Brassospora* [Philipson and Philipson 1988; Hill and Read 1991]) is particularly abundant. Similarly, the affinities of the gymnosperms lie with taxa from generally low latitude (e.g. *Dacrydium* s.l. and Araucariaceae) to high latitude (e.g. *Lagarostrobos franklinii* and *Microcachrys tetragona*) environments. Modern associations containing mixtures of these elements occur in montane tropic regions of New Guinea and New Caledonia, and temperate rainforests of northern New South Wales, Tasmania, New Zealand and Chile/Argentina. It is therefore certain that the vegetation surrounding the depositional site at Cethana included microthermal rainforest dominated by these taxa. This scenario is thus very similar to that described by Hill and Macphail (1983) for the Tasmanian Oligocene Pioneer flora, where a diverse cryptogam flora including tree -ferns, mosses and lycopods occupied the understorey and epiphytic niches of a cool closed forest which also included *Quintinia*, Proteaceae, Epacridaceae, Casuarinaceae and Myrtaceae. A key indicator taxon for the Oligocene of south-eastern Australia, *Cyatheacidites annulatus*, has been shown conclusively by Dettmann (1986) to be referable to the tree-fern *Lophosoria quadripinnata*, which is now restricted to cool, mesic regions of South and Central America. The only known living species

Figure 2. ***Nothofagus*** **and conifer pollen**

Figs a-d, f, i, l, m. Scanning Electron Micrographs (SEM's).

Figs e, g, h, j, k, n. Light Micrographs (LM's) (all scale bars 10 μm).

a. *Nothofagidites falcatus.*

b. *Nothofagidites heterus.*

c. *Nothofagidites flemingii.*

d. *Podocarpidites* sp.

e. *Nothofagidites deminutus.*

f. *Nothofagidites asperus.*

g. *Podosporites microsaccatus.*

h. *Microcachyridites antarcticus.*

i, j. *Phyllocladidites mawsonii.*

k. *Lygistepollenites florinii.*

l. *Araucariacites australis.*

m, n. *Podocarpidites* sp.

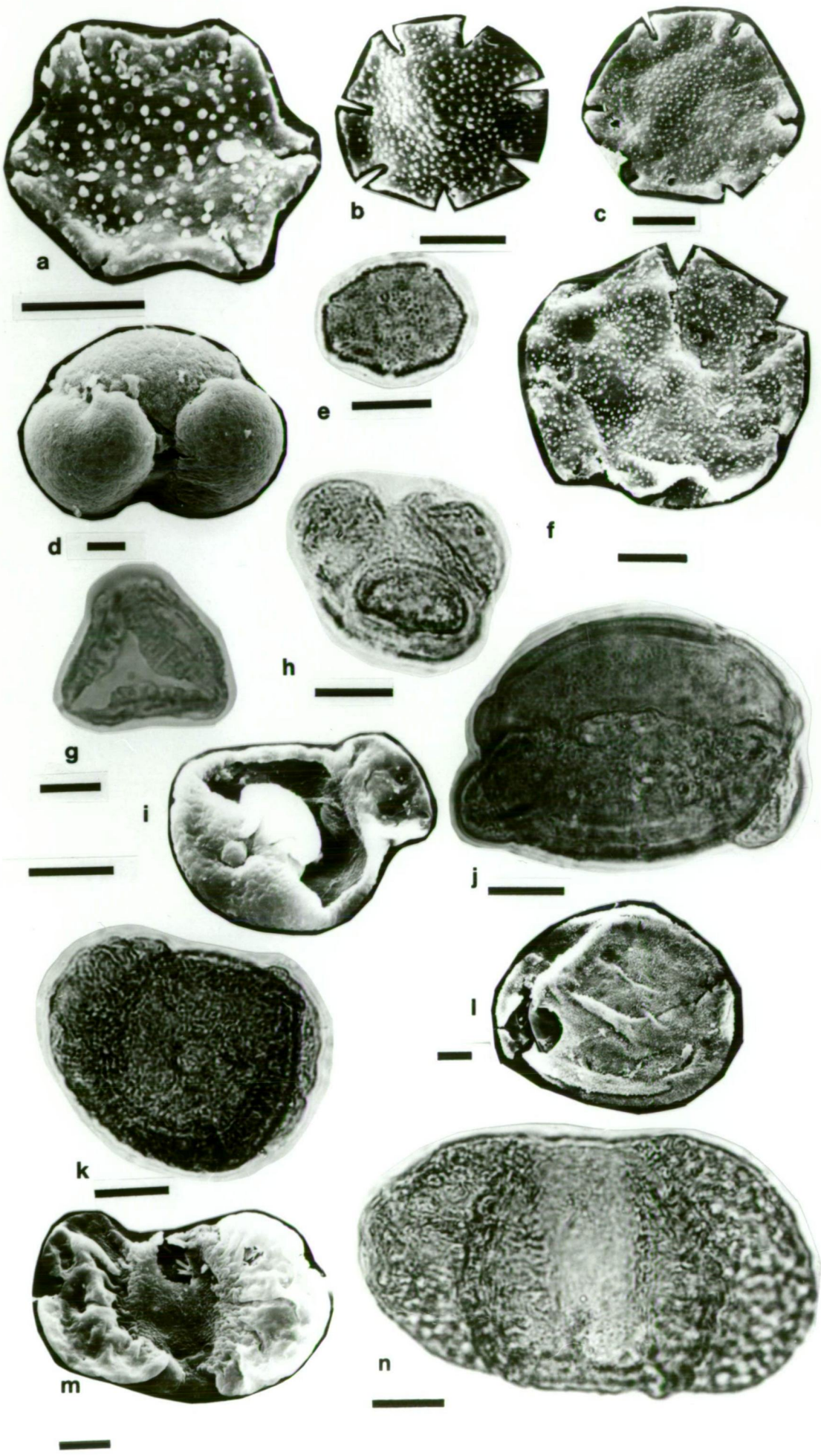

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Figure 3. Pollen and spores

Figs a, c-f, h-j, m. LM (all scale bars 10 μm).

Figs b, g, k, l. SEM (all scale bars 10 μm).

a. *Gleicheniidites circinidites.*

b. *Proteacidites* sp.

c. Droseraceae.

d. *Periporopollenites vesicus.*

e. *Tricolporites* sp.

f. *Haloragacidites harrisii.*

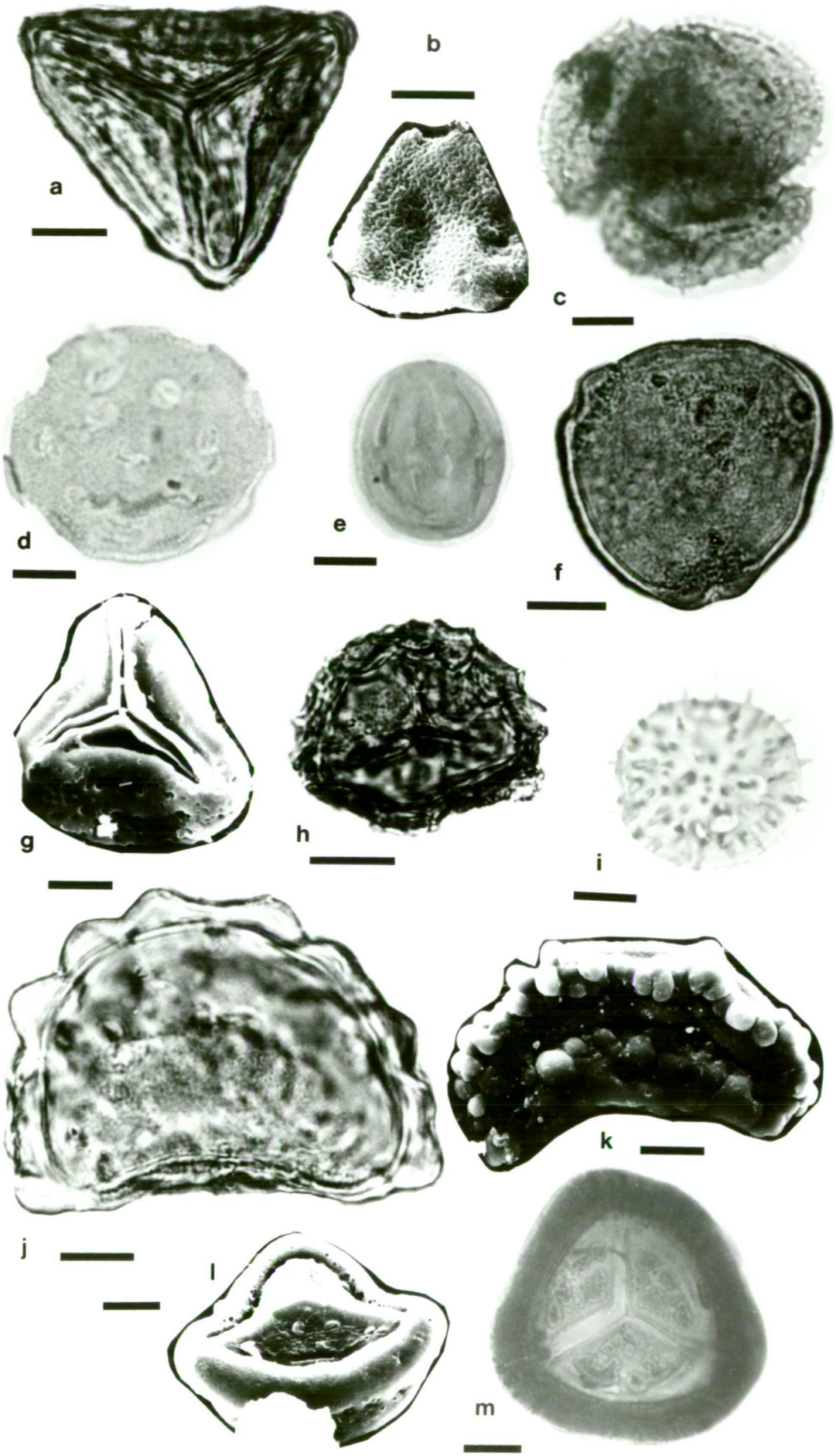
g. *Cyatheacidites* sp.

h. *Lycopodiumsporites* sp.

i. *Malvacipollis subtilis.*

j, k. *Verrucatosporites attinatus* n. var.

l, m. *Cyatheacidites annulatus.*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producing the *Granodiporites nebulosus* pollen type is *Embothrium coccineum* (Macphail and Truswell 1989; Feuer 1989). This species is now restricted to Chilean microthermal rainforest.

Other elements of interest include Gunneraceae and Droseraceae. These taxa, along with Restionaceae and some ferns such as Gleicheniaceae could have occupied open, boggy and infertile regions proximal to the lake where deposition occurred.

No pollen from Poaceae, Compositae, or Leguminosae was recorded. Hence, there is no evidence for the existence of grasslands or a semi-arid habitat in the region, since members of these families dominate such regions today. Similarly, so-called 'warm' indicator taxa such as Cupanieae, Malvaceae, Bombacaceae, *Beauprea* (Proteaceae) and *Anacolosa* (Kemp 1981) have not been found in the Cethana sediments. Although negative evidence may be uninformative, particularly given the poor preservation at Cethana, this suggests that the vegetation of the region was not growing under the type of conditions which today occur in the lowland tropics.

The palynoflora also includes numerous cysts of an undescribed freshwater dinocyst comparable with *Saeptodinium* (M. K. Macphail, personal communication).

CHAPTER 4

MACROFOSSILS

4.1 INTRODUCTION

Numerous Australian Tertiary plant fossil deposits are currently being investigated, but although many have a high diversity of very well preserved macrofossils, comparatively few taxa have been identified and formally described. Exceptions are in the gymnosperm families Zamiaceae, Araucariaceae, Podocarpaceae and Cupressaceae where species from numerous genera have been described (e.g. Cookson and Duigan 1951; Cookson 1953a; Cookson and Pike 1953a, 1953b; Townrow 1965a; Hill 1978, 1980, 1989a; Greenwood 1987a; Bigwood and Hill 1985; Carpenter 1991-appendix I; Hill and Carpenter 1989-appendix II; Wells and Hill 1989a). This is partly because these elements are often abundant and well preserved and also because important details of the extant taxa (such as cuticular micromorphology) are well known (e.g. Florin 1940; Stockey and Ko 1986; Wells and Hill 1989b).

Recent papers describing Tertiary angiosperms are comparatively few, considering the apparent diversity of taxa [e.g.Christophel (1981) recognises over 200 leaf types from the Eocene Maslin Bay deposit]. The best understood groups are the Banksieae (Proteaceae) (Cookson and Duigan 1950; Christophel 1984; McNamara and Scott 1983, Hill and Christophel 1988; Hill 1990b) and *Nothofagus* (Hill 1983a, 1983b, 1984, 1987, 1991a; Christophel 1985), although macrofossils of *Lomatia* (Proteaceae) (Carpenter and Hill 1988), Myrtaceae (Christophel and Lys 1986), Ebenaceae (Christophel and Basinger 1982; Basinger and Christophel 1985), Araliaceae (Blackburn 1981), Casuarinaceae (Christophel 1980), Lauraceae (Hill 1986, 1988a), Menispermaceae (Hill 1989b) and *Eucryphia* (Eucryphiaceae) (Hill 1991b) have been described. Other Tertiary angiosperm taxa known to occur as organically preserved macrofossils, though not formally described are *Quintinia* (Christophel *et al.* 1987), Elaeocarpaceae aff. *Sloanea/Elaeocarpus* and *Brachychiton* (Sterculiaceae) (Christophel and Greenwood 1987).

Pteridophyte macrofossils are apparently not well represented in Australian

Tertiary deposits, and recently only *Isoetes* (Isoetaceae) (Hill 1988b), *Tmesipteris* (Psilotaceae) (Carpenter 1988) and *Lygodium* (Schizaeaceae) (Churchill 1969) have been described, although the latter genus has been found in several Eocene deposits (Christophel 1989).

In the account of the Cethana macroflora in this study representatives of most of the taxa referred to above have been identified as well as many taxa which have no previous fossil record in Australia.

4.2 METHODS AND MATERIALS

Blocks of fossiliferous sediment were collected from Cethana and removed to the laboratory for analysis. No sediments containing mummified material were found. The best method for exposing the macrofossils was to allow the blocks to dry over a period of several months, and then split them with a sharp bladed mallet. Straight cleavages (and hence rapid accumulation of specimens) were difficult to obtain because of the siliceous debris described previously and their effect of disrupting the sedimentary layers. Macrofossil specimens were numbered and catalogued as they were discovered.

The Cethana macrofossils usually exist as impressions but organic fragments could often be recovered from compression fossils. These fragments were washed in hydrofluoric acid (HF) to remove adhering siliceous material and then prepared in one of two ways for microscopic study. The first option was to place the pieces in 10% chromium trioxide (CrO_3) solution. The advantage of using this solution was first indicated by Alvin and Boulter (1974), and has since been advocated by Stockey and co-workers (e.g Stockey and Ko 1986) and Wells and Hill (1989a, 1989b). In most instances clean cuticles separated from the carbonised remains within 24 hours. However, for some specimens better preparations were obtained by placing fragments in nitric acid and potassium chlorate (Schulze's solution) until all the organic material except the cuticle had dissolved. Regardless of clearing technique cuticles were then washed in water and dilute ammonia and either stained with 1% Safranin O and mounted in phenol glycerin jelly for light microscopy, or mounted on double-sided

adhesive tape on metal stubs and air-dried for scanning electron microscopy. Stubs were then sputter-coated with gold to a maximum thickness of 20 nm and examined with a Philips 505 Scanning Electron Microscope operated at 15 kV.

Some dispersed cuticle slides were also prepared. Samples of sediment rich in organic remains were placed in a 200 ml beaker in a solution of neutral detergent and hot water and agitated until the sediment had reduced to a slurry. This was then sieved, and the black organic chips rinsed into a beaker for processing as outlined above. Material from the apparently lignitic sediments referred to in Chapter 2 was also treated but no cuticular remains discovered.

Fossils were photographed using reflected light. Low-angle illumination or camera lucida drawings were sometimes used to emphasise features such as leaf shape, shoot phyllotaxy, and venation.

Extant material for comparison to the fossils was obtained from herbarium specimens and cuticles prepared using the CrO_3 treatment.

4.3 IDENTIFICATION AND NOMENCLATURE

Collinson (1986) discussed the use of modern generic names for plant fossils and contended that "if a thorough and critical comparison is made and the diagnostic suite of characters exhibited by a plant fossil organ falls within the range of those of a certain taxon of modern material (and not within those of any other modern material) then there is no reason to assume the two are different but good reason to assume they can be identified to the same taxon". This philosophy is adopted in this study. Where a taxon name is used unqualified it implies a very high probability that the fossil taxon belongs to the named extant taxon whether of familial, generic or specific rank. Where a fossil organ agrees in all available information with a comparable modern (or another fossil) organ, but it is considered that certain information diagnostic in these is lacking or incomplete, the prefix 'aff.' is used to denote the uncertainty. Similarly, this prefix is used if for instance the cuticular morphology of comparable modern taxa has not been studied in sufficient detail to establish diagnostic characters or where modern taxonomic relationships are poorly understood. The prefix '?' is used when a

specimen exhibits morphological similarity to a certain taxon, but the degree of certainty of identification is less, because for instance reproductive structures or cuticular preservation are completely lacking.

Fossil identification often depends entirely on isolated leaves which may be represented by one or only a few specimens. Therefore, as many characters as possible should be assessed. These include aspects of leaf size and shape, venation and tooth architecture (Hickey 1979). A diverse array of important characters may be found on the cuticle (Stace 1965; Dilcher 1974) and these include the distribution of stomates, the arrangement of subsidiary cells, the presence and nature of trichomes or papillae and various other surface ornamentations such as striations on the outer surface and granulations on the inner surface. Significantly, many of these features are genetically fixed, and thus are potentially important for taxonomic and phylogenetic studies. Understanding of cuticular micromorphology has been greatly enhanced with the use of the SEM since it enables the often complex microrelief of both inner and outer surfaces to be observed. The diagnostic characters of some Australasian taxa are already well known. For instance, Johnson and Briggs (1975) note that the Proteaceae has characteristic paracytic stomates and trichomes which are found in all genera. Most of what is already known about cuticle morphology of this family has stemmed from palaeobotanical research. For instance, Cookson and Duigan (1950) examined the cuticular structure of species in the tribe Banksieae. Using a reference set of extant species Lange (1978) found several dispersed Eocene cuticles to be comparable to Proteaceae but was generally pessimistic about the prospects of using cuticles for taxonomic purposes. However, numerous recent studies, of both living and fossil taxa, and concerning both angiosperms and gymnosperms, have demonstrated the validity of the technique, particularly when use is made of the SEM. Examples include several studies within the Podocarpaceae and Araucariaceae. Examination of all modern species of *Araucaria* by Stockey and Ko (1986) showed that consistent differences in epidermal cell and stomatal apparatus micromorphology could be used to distinguish the four sections of the genus. This information coupled with the fact that *Araucaria* and *Agathis* species have distinct stomatal orientations

(Cookson and Duigan 1951; Bigwood and Hill 1985) enabled others, including Hill (1990c), to readily assign fossil species to modern sections and suggest their nearest living affinities. Wells and Hill (1989a) showed that all genera of the imbricate Podocarpaceae, including the problematical Group C *Dacrydium* taxa, could be separated on the basis of cuticle morphology alone. Hill and Read (1991) have proposed an infrageneric revision of *Nothofagus* in which each subgenus possesses distinctive leaf cuticular characters and cupule morphology. In another recent study Sampson *et al.* (1988) erected a new species of *Tasmannia* (Winteraceae), differing in epidermal characters from all other Australian species in having a papillate lower epidermis and distinctive cuticular striations on the upper surface.

Macrofossil identifications based on architecture alone may lead to erroneous palaeoecological conclusions. An example where this could happen is in the interpretation of *Banksieaephyllum* (Proteaceae) leaves from Australian Early Tertiary sediments. Some species of this genus have leaves with an identical gross morphology to those of extant species of *Banksia* and *Dryandra*, but differ significantly in that the stomates of the fossils are quite superficial. The extant plants often have stomates sunken in deep hair-filled pits and are found in regions which experience hot and dry summers. Therefore, if the fossil cuticles were not examined, one could have been led to the conclusion that a similar climate prevailed in the Early Tertiary, when in fact it was probably everwet. Thus, apart from their taxonomic significance plant cuticles can reveal much about the prevailing environment.

It is beyond the scope of this study to formally describe each taxon. In general, those described in this manner are fossils with exceptional preservation enabling detailed cuticular analysis and which are considered to be significant in being unique records and/or providing important biogeographic and ecological information. Otherwise, only a brief informal description is provided. However, there is no doubt that many of these taxa can confidently be ascribed to extant genera, and in some cases, affinities at the specific level are suggested and ecological conclusions drawn. Terminology for the fossil descriptions generally follows Hickey (1979) for leaf architecture and Dilcher (1974) for cuticle morphology. Although it is impossible to

be certain which were the upper and lower surfaces of the fossil leaves in the Cethana flora it is assumed that for angiosperms the surface with the most stomates is the abaxial surface.

Various limitations apply to the results of this research. The species described herein are usually represented by only one or a few specimens each, and cuticular preservation is sometimes lacking. In addition, where cuticle is present it is often fragmentary and this means that, for instance, it is exceedingly difficult and time-consuming to determine the complete distribution of stomates on a leaf surface.

The concepts of cladistic phylogeny have recently been adopted by many systematists. Essentially, groups of taxa are hierarchically classified according to the presence of shared derived characters (synapomorphies). Conversely, shared ancestral traits (symplesiomorphies) are considered to be uninformative for interpreting evolutionary processes. It is well beyond the scope of this study to analyse the phylogenies of the taxa identified. Donoghue (1989), who has published several papers on the cladistic phylogeny of plant groups, notes that "cladistic analysis is a time-consuming and onerous task, and even in the best of cases, uncertainties are likely to persist concerning both cladogram topology and character optimization." Few groups relevant to the flora described in this study have been treated cladistically. An exception is *Nothofagus*, though in these analyses (e.g. Humphries 1983) lies what is perhaps the greatest potential trap for cladists- the use of incorrect data and inappropriate choice of character polarity. Hill and Read (1991) listed numerous examples of such errors in previous cladistic analyses of the genus. In addition, it is evident that Australian Oligocene floras are composed of many taxa (including species with excellently preserved cuticles) which are virtually indistinguishable from modern species. Thus the task is generally one of identification, not phylogenetic interpretation of suites of new fossil genera and families with intermediate characters. Notwithstanding this, it is recognised that all botanical research will benefit greatly from the important philosophical contributions to the understanding of evolution offered by cladistics.

In contrast to theoretical biogeographic approaches, whether they be narrative or

based on rigorous cladistics, thorough Tertiary palaeobotanical studies will provide unequivocal records of past floras and climate. They seek to integrate aspects of geology, ecology, climate and physiology in understanding the changes in vegetation through time. Wolfe (1987) points out that on the other hand, cladistic biogeographers have often ignored the fossil record. They have considered the history of the physical environment solely in terms of plate tectonics without acknowledging the importance of climate changes.

4.4 MACROFOSSIL TAXONOMY

4.4.1 PTERIDOPHYTA

Taxonomy follows the treatment of Australian ferns by Jones and Clemesha (1980) but other taxonomic literature (e.g. Holttum 1959a, 1959b, 1963; Tryon and Tryon 1982) was also consulted. No cuticular remains or spores from reproductive structures have been obtained. An unidentified isolated sporangium is illustrated in Fig 4a. Generally, pteridophyte taxonomy is based on the morphology and arrangement of reproductive structures but there is no doubt that certain vegetative features are of diagnostic value, and these are referred to where appropriate.

Order Psilotales

Family Psilotaceae

Tmesipteris Bernh.

Tmesipteris tasmanica R. J. Carpenter

Specimen examined. C-204

This species was described and discussed by Carpenter (1988).

Order ? Blechnales

Family ? Blechnaceae

? ***Blechnum*** L.

Specimens examined. C-083, 420, 530, 531

Description. Incomplete pinnae have been recovered and are up to 18 mm

wide with a costa about 0.5 mm wide, and at least 60 mm long (probably much longer since the margins of this specimen were parallel). The apex is acuminate and the margin is regularly and finely toothed. The lateral veins arise at an angle of 40-70° and terminate in the tooth sinuses. They are usually simple but some fork near the costa. C-530 is illustrated in Fig. 4b. On two specimens each vein near the margin discernably widens into an elongate impression about 0.5 mm long (Fig. 4c).

Discussion. The specimens are morphologically identical to the infertile fronds of what is apparently a very closely related group (Duncan and Isaac 1986) of extant *Blechnum* species. This group comprises *B. wattsii* Tindale (Fig 4d) (common in south-eastern Australia), *B. vestitum* of the mountains of Malaysia (Holttum 1954) and *B. procerum* (Forst. f.) Sw. of New Zealand and *B. capense* (L.) Schlecht. of South Africa (Brownsey *et al.* 1985). However, no fertile blechnaceous foliage has been recognised in the Cethana sediments, and so the specimens cannot be referred to the genus with absolute confidence. The form of venation and toothed margin of these pinnae may be found in other ferns including infertile fronds of *Marattia* (Marattiaceae) and *Angiopteris* (Angiopteridaceae), but the conspicuous manner in which the veins widen near their termination with the tooth sinuses is not found in these genera. Holttum (1954), in his description of *B. vestitum*, regarded the widened vein region as a large hydathode. In contrast, the veins of *Marattia* and *Angiopteris* terminate in the tooth apices. *Blechnum* is primarily a genus of wet mountain forests of the tropics (Tryon and Tryon 1982), but many species do occur in Tasmania.

Order ? Cyathales

Family ? Cyatheaceae

Specimens examined. C-255, 446

Description. The two specimens are fragments of fronds (pinnules) lacking reproductive structures (Figs 4e, f), the largest being 45 mm long, including a 3 mm long base. The two pinnule sections have six and seven opposite or almost opposite deep lobes, to about 1.5 mm from the costa, with costules spaced approximately 7 mm apart and up to nine pairs of free veins, which, with the exception of the apical ones

Figure 4. Pteridophyta

a. SEM of an unidentified sporangium portion. Note the prominent annulus. Scale: 100 μm.

Figs b, c. ? *Blechnum* sp. (p. 25)

b. C-530. Toothed segment of pinna. Scale: 10 mm.

c. C-420. Note the vein impressions terminating in hydathodes. One of these is arrowed. Scale: 1 mm.

d. Extant *Blechnum wattsii*. Pinna segment. Note the venation and small hydathodes. Scale: 10 mm.

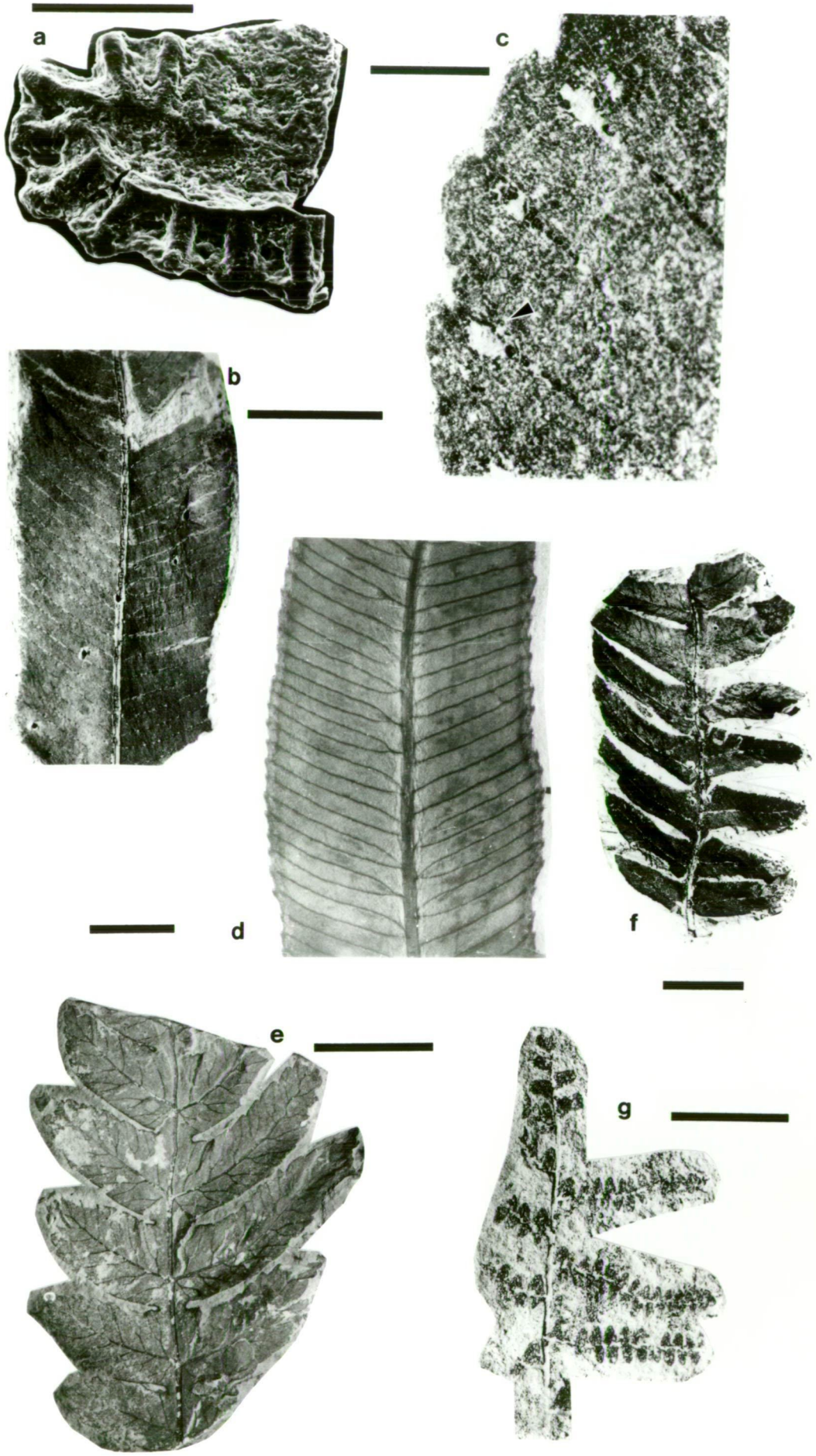
Figs e, f. ? Cyatheaceae. (p. 26)

e. C-255. Scale: 10 mm.

f. C-446. Scale: 10 mm.

(p. 28)

g. *Gleichenia* sp. (C-099). Scale: 10 mm.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are once-forked. The basal basiscopic veins arise at the junction of the costa and costules. The lobes are slightly falcate to the acute apex and the margins are distinctly toothed. The lobes are slightly enlarged at the base and up to 18 mm long, the lower ones of the specimen with the petiole base being shorter.

Discussion. In the absence of reproductive material the precise affinities of the fossils are impossible to determine. However, their vegetative morphology is entirely consistent with species of *Cyathea*, as described for instance by Holttum (1963) and Jones and Clemesha (1980). Despite this, the possibility that the specimens belong to another fern genus, particularly another tree fern such as *Dicksonia* or *Culcita* (Dicksoniaceae) should not be discounted. Most tree fern species are found in the wet tropics of Australasia, especially on mountains (Holttum 1963). Cyathea now has a limited distribution in Tasmania, but C.australis is common in southeastern Australia generally.

Order Gleicheniales

Family Gleicheniaceae

Australian taxonomic treatments of the Gleicheniaceae regard species with very small pinnule lobes as *Gleichenia* with the other genera in the family being *Sticherus*, *Diplopterygium* and *Dicranopteris* (Jones and Clemesha 1980). These ferns possess the absolutely diagnostic character of repeated pseudodichotomous forking of the rachis. Holttum (1959a) recognises only two genera, *Dicranopteris* and *Gleichenia*, with *Gleichenia* having three subgenera. Subgenus *Mertensia* is equivalent to *Sticherus* and subgenus *Gleichenia* includes the Australian *Gleichenia* species. A feature which can be used to separate *Sticherus* and *Dicranopteris* is that the secondary veins of the latter are forked two to five times, whereas those of *Sticherus* are forked only once (Jones and Clemesha 1980). *Sticherus* (or *Gleichenia* subgenus *Mertensia*) can be distinguished from *Diplopterygium* (or *Gleichenia* subgenus *Diplopterygium*) since the latter exhibits a different branching pattern and its ultimate frond segments are not as deeply cut to the rachis as those of species of *Sticherus* (Holttum 1959a). At Cethana both *Gleichenia* and *Sticherus* occur.

Gleichenia J. Sm.

Gleichenia sp.

Specimens examined. C-048, 099

Description. Specimen C-099 is the section of an alternately branched pinna 35 mm long (Fig. 4g). Pinnule branches occur at right angles to the main axis and are up to 13 mm long. The pinnules are divided into small rounded lobes, typically about 1.5 mm broad at the base and 1.5 mm long.

Discussion. Although reproductive structures have not been discerned, the fossil can readily be assigned to generic level on the basis of its highly distinctive vegetative morphology where the presence of small lobe-like pinnules on the bipinnate ultimate branch is diagnostic. In all there are only about 10 extant species in this group, found in tropical and southern Africa, the Mascarene Islands, Malaysia and Australasia (Holttum 1959a). In Australia the genus is found in a variety of open habitats such as swamps, rainforest margins, sclerophyll forests and wet crevices in rock faces (Jones and Clemesha 1980). In the Malesian tropics species are found only on exposed mountain summits and ridges, often on sandstone or quartzite (Holttum 1959a). A few *Gleichenia* species are found in cool and cold temperate regions of New Zealand and Tasmania (Jones and Clemesha 1980). *Gleichenia* macrofossils have also been reported by Cookson (1953b) from Early Tertiary sediments in South Australia and Blackburn (1985) from Yallourn and Morwell coals in Victoria.

Sticherus Presl

Sticherus sp.

Specimens examined. C-253, 593, 637

Description. Specimen C-593 is represented by a frond segment with many entire margined pinnules with rounded apices, up to 10 mm long and about 2.5 mm wide at the base, which bear the impressions of sporangial attachment regions and once forked veins (Fig. 5a). Four to six pairs of sori occurred in single rows on the acroscopic branches of these veins. The other specimens lack reproductive structures but their vegetative features indicate a clear affinity to *Sticherus* and there is no reason

Figure 5. Pteridophyta

Figs a-c. Sticherus sp. (p. 28)

a. C-593. Section of pinnule showing the impressions of soral sites (one on the lower right side is arrowed) on the acroscopic branches of once-forked veins (apex uppermost). Scale: 1 mm.

b. C-253. Scale: 10 mm.

c. C-637. Note the once-forked veins. One of these on the lower right side is arrowed. Scale: 1 mm.

(p. 29)

d. aff. *Hymenophyllum* (C-635). An indusium is arrowed. Scale: 1 mm.

Figs e, f. *Schizaea* sp. (C-071). (p. 30)

e. Whole specimen showing sterile fronds. Scale: 10 mm.

f. Enlargement to show dichotomies and the truncate apices of the fronds. Scale: 5 mm.

(p. 31)

g. *Lygodium* sp. (C-232). Scale: 10 mm.

h. C-592. Compare to **Fig. 5g** and note the presence of a distinct petiole, pronounced costa, toothed margin and twice dichotomising veins. Scale: 10 mm.


a
b
c
d
e
f
g
h

to doubt conspecificity with C-593. Specimen C-253 is represented by what is presumably a pair of ultimate segments, branched at about 45° and each in turn bearing pinnules diverging at 45-60° from the rachis (Fig. 5b). The entire margined pinnules are about 16 mm long and 5 mm wide at the base, which may be slightly expanded. They taper gradually to the rounded apex. The only obvious venation is a costa in each pinnule but once forked secondary veins are discernible using low angle lighting. Fig. 5c shows the obvious once forked veins of specimen C-637.

Discussion. The fossil specimens have only once-forked lateral veins in their pinnae. The pinnae are divided to the rachis and there is an identical branching pattern to that illustrated by Holttum (1959a) for subgenus *Mertensia.* In addition, the site and apparent nature of the soral attachments observed in C-593 conforms entirely to the genus. The specimens can therefore be assigned to *Sticherus* with confidence. Of the extant Australian species the Cethana specimens exhibit a remarkable similarity to extant *Sticherus tener* (R. Br.) Ching from south-eastern Australia (Jones and Clemesha 1980). Hill (1980) suggests *Sticherus flabellatus* (R. Br.) St. John as an affinity for a fossil fern frond fragment from the Eocene Nerriga deposit of New South Wales. There are no other Australian macrofossil records. Extant *Sticherus* species (and indeed all Gleicheniaceae with the exception of *Dicranopteris*) are typically found in temperate high latitude regions or at high altitude in the tropics. All species in the family are sun ferns and most are pioneer plants of bare ground or rock such as talus, precipices, steep ridges and landslides (Holttum 1959a). The soils in these areas are usually shallow and highly leached.

Order Hymenophyllales

Family Hymenophyllaceae

aff. ***Hymenophyllum*** L.

Specimen examined. C-635

Description. The 7 mm long section is illustrated in Fig. 5d. It may be the major portion of a pinnule or small pinna or the apical segment of a pinna or frond. Each of the lateral segments from the main axis is about 2-3 mm long and the lobes

less than 1 mm wide. A single vein trace is visible in each lobe. The margins are entire. Terminating the lobes of the upper margin of the lateral segments are flask-shaped indusia approximately 0.5 mm wide and 1 mm long (Fig. 5d).

Discussion. The morphology of the segment of frond and its reproductive structures as described shows clear affinity to the Hymenophyllaceae, and probably *Hymenophyllum*, since there is no evidence of exserted receptacles on the sori. These are a diagnostic character of the other major genus *Trichomanes* and exist as prominent bristle-like protruberances from the lip of the indusia (Jones and Clemesha 1980; Duncan and Isaac 1986; Tryon and Tryon 1982). On the other hand the indusia of the fossil have left a distinctive flask shaped impression, which is more typical of *Trichomanes*, and it is possible that the receptacles were detached by taphonomic processes. A sample of sediment and organic material from the region of an indusium was searched for spores but none were found. The Hymenophyllaceae is notable for the fact that the fronds may be only a single cell thick, and consequently these ferns are restricted to continuously damp habitats. *Hymenophyllum* is best developed in wet north and south temperate regions and in the montane tropics. In tropical America the genus is most common in cloud forests and wet montane forests of Andean Colombia to Peru at altitudes from 1500-2000 m (Tryon and Tryon 1982). No other macrofossil records are known.

Order Schizaeales

Family Schizaeaceae

Schizaea J. Sm.

Schizaea sp.

Specimen examined. C-071

Description. The fossil consists of sterile fronds about 1 mm wide, which dichotomise up to at least four times (Fig. 5e, f). Impressions are left by the costae, which appear to narrow or disappear in the ultimate branches or as the blades of these widen. The apices of the ultimate branches are truncate or slightly rounded.

Discussion. The presence of distinctive filiform, repeatedly dichotomising

fronds enable confident assignment of this specimen to *Schizaea* and suggest an affinity to *S. dichotoma* (L.) Sm. or *S. asperula* Wakefield, the only species in the Australasian region with such a degree of dichotomy (Holttum 1959b; Duncan and Isaac 1986). *Schizaea* is a pantropic genus, which is also widely distributed in temperate regions of the southern hemisphere, and comprises about 30 species (Holttum 1959b). *S. dichotoma* may be found from sea level to 1000 m in northern Australia, Southeast Asia and the Pacific and according to Jones and Clemesha (1980) *S. asperula* is restricted to south-eastern Australia and New Zealand. Species of *Schizaea* are apparently confined to open vegetation on nutrient deficient soils, typically sands. No other macrofossil records are known.

Lygodium Sw.

Lygodium sp.

Specimens examined. C-232, 661

Description. Specimen C-232 is represented by a lobed sterile leaflet about 35 mm long and 9 mm wide (Fig. 5g). The veins usually dichotomise three times, and rarely four times, after arising at about 10-20° from the poorly defined costules. The veins do not anastomose. The margin is irregularly crenate and the apex of the leaflet is obtuse. C-661 is incomplete at the base but is undoubtedly conspecific. The portion is 42 mm long and 17 mm wide.

Discussion. The gross morphology and repeatedly dichotomising high angle venation of the specimens indicates that this taxon can be referred to *Lygodium* with confidence. However, the lack of fertile material makes determination of specific affinities impossible.

Several other specimens (C-256, 452, 592 [Fig. 5h], 660) bear some similarity to *Lygodium* foliage, but are clearly distinct from those specimens assigned to this genus. These leaflets are about 35 mm long and 7 mm wide with a 2-5 mm long petiole and are ovate to lanceolate. They differ from the confidently identified *Lygodium* species in four features, which suggest that if they belong to *Lygodium*, then they belong to a distinct species. These features are; 1) simple leaflets with a

distinct petiole, 2) the costa is pronounced and becomes less distinct near the acute apex, 3) the margin is distinctly toothed with several veins terminating at the margin per tooth and 4) the veins only dichotomise twice. This taxon is somewhat enigmatic in that its features conform exactly to the expanded description of *Phyllopteroides* by Cantrill and Webb (1987). This genus is known from the Early Cretaceous of Victoria and Queensland, and was considered by these authors to be osmundaceous. Churchill (1969) also discusses previous records of sterile foliage attributed to *Lygodium* and notes the similarity of *Osmunda* and *Lygodium*. The possibility that this Cethana taxon belongs to the Osmundaceae should not be discounted.

Lygodium species are light requiring twining climbers of open shrubby vegetation or rainforest margins, usually in the tropics. In Australia the genus is resticted to Queensland, and northern areas of New South Wales, Western Australia and the Northern Territory (Jones and Clemesha 1980). An endemic species does however occur in the North Island of New Zealand (Allan 1961). *Lygodium* impressions, frequently with fertile leaflets, have been found in Late Cretaceous and Early Tertiary rocks from Chile (Halle 1940), Europe and North America (Holttum 1959b; Manchester and Zavada 1989). Ettingshausen (1888) described *L. strzeleckii* from Vegetable Creek, New South Wales, and Churchill (1969) described *L. dinmorphyllum* from an Eocene-Oligocene deposit in Queensland which he concluded was most similar to the extant New Zealand species, *L. articulatum* A. Rich. Fossil leaflets are also known from several other Eocene deposits in Australia (Greenwood and Christophel 1988).

4.4.2 GYMNOSPERMAE

Order Cycadales

Family Zamiaceae

Macrozamia Miq.

Macrozamia australis R. J. Carpenter

Specimens examined. C-532, 651, 652

This species was described and discussed by Carpenter (1991-appendix I).

Family ? Zamiaceae

Pterostoma R. Hill

Pterostoma aff. *anastomosans* R. Hill

Specimens examined. C-483

Description. The specimen consists of a pinnae fragment 42 mm long and 12.5 mm wide (Fig. 6a). It tapers slightly, to 10.5 mm, at one end. This is the basal end since occasional vein dichotomies have been observed. At any point there are about 16 veins across the width of the pinna, or about 13 per cm. Vein anastomoses are probably absent, but the specimen is coated with small organic fragments and abundant resin which would tend to mask the presence of minor vein anastomoses. On the abaxial surface the stomates are randomly orientated (Fig. 6b). They are identical in morphology and dimensions to those of *Pterostoma anastomosans* described by Hill (1980). Subsidiary cells are not discernible because of the cuticular surface thickenings around the stomates (Fig. 6c). Highly developed cuticular ridges occur all over the epidermal surface and radiate from the circular scars of trichome bases. These are single celled and are most frequent over veins. The ratio of stomates to trichome bases is approximately 1 : 4. On the inner adaxial surface the epidermal cell walls are highly sinuous (Fig. 6d). The outer cuticular surface is featureless and trichome bases were not observed. No cuticle fragments large enough to assist in determining the status of vein anastomoses have been recovered.

Discussion. *Pterostoma* is an extinct genus containing two species from two Eocene deposits of south-eastern Australia and was tentatively included in the

Figure 6. Order Cycadales

Figs a-d. *Pterostoma* aff. *anastomosans* (C-483). (p. 33)

a. Pinna fragment. Note tapering to one end and vein impressions. Scale: 10 mm.

b. SEM of inner surface of abaxial cuticle showing stomates and a large trichome base on the left hand side. Scale: 10 μm.

c. SEM of outer abaxial surface showing prominent cuticular ridges and a stomatal opening. Scale: 10 μm.

d. SEM of inner surface of adaxial cuticle, showing sinuous walls. Scale: 10 μm.

Figs e-h. ? cycad. (p. 35)

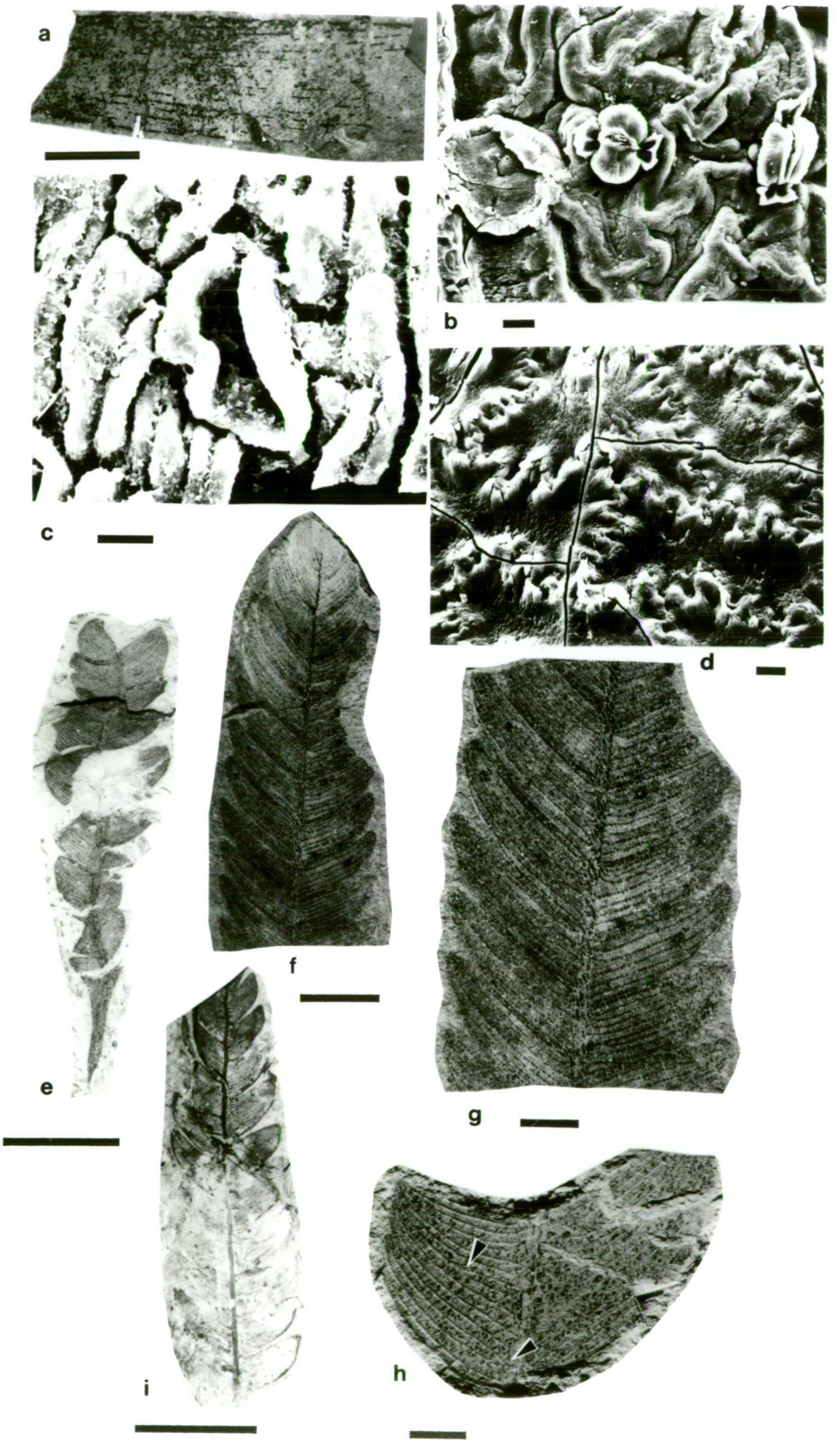
e. C-258. Note the leaf base. Scale: 10 mm.

f. C-455. Scale: 5 mm.

g. Enlargement of **Fig. 6f** to highlight venation. Scale: 2 mm.

h. C-347. Note the single vein anastomosis and a vein dichotomy (both arrowed). Scale: 2 mm.

i. Specimen of *Anomozamites muelleri* from Vegetable Creek. Scale: 10 mm.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Zamiaceae by Hill (1980). The fronds of these plants are highly distinctive, possessing frequently dichotomising and anastomosing venation and cuticles with randomly arranged stomates, highly sinuous epidermal cell walls and pronounced surface ridgings. Hill (1980) recognised this combination of features and suggested that *Pterostoma* may be closely related to species of *Ctenis* which apparently became extinct in the Cretaceous. Pant (1987) reassigned *Pterostoma* to *Macrozamia* on the basis of the presence of sinuous cell walls and what he believed to be a similarity of frond architecture. He apparently overlooked the much more distinctive features outlined above. In any event, the presence of sinuous anticlinal cell walls is hardly a diagnostic character, and Hill (1980) stresses that the rachis bases of *Pterostoma* are swollen into an abscission layer, indicating that they were probably deciduous, a feature unknown in modern cycads. Pant's proposal is therefore rejected.

In his description of *P. anastomosans* Hill (1980) noted a network of frequently anastomosing fine veins running between the major veins. This distinctive character, along with the distribution of trichome bases was used to separate the two *Pterostoma* species he described. Trichome bases are absent from the abaxial epidermis of *P. zamioides*. Because of the nature of fossilization vein details are not observable in the Cethana specimen. However, the observed cuticular features are indistinguishable from those described for *P. anastomosans*, with the exception that the trichome bases of the Cethana fossil are all single celled whereas those of *P. anastomosans* are two-to-three celled. Therefore, an affinity to this species is recognised but the species are probably distinct, a likelihood increased by the fact that the deposits from which the fossils were recovered are spatially and temporally distinct. *Pterostoma anastomosans* was recorded from the Middle Eocene Nerriga deposit of New South Wales, which Hill (1982, 1986) considered to have been deposited under warm sub-tropical conditions in which the Lauraceae were a dominant component of the surrounding vegetation. Only one small pinna fragment was recovered. The other described species, *P. zamioides*, is common in the late Middle Eocene Anglesea deposit of Victoria, especially in lenses with abundant *Gymnostoma* (Casuarinaceae) remains (Hill 1980; Christophel *et al.* 1987). The genus has since been recorded from

Miocene sediments of Yallourn, Victoria (D. R. Greenwood, personal communication) and one other Tasmanian Eocene deposit. Therefore, it is evident that these plants were a component of south-eastern Australian vegetation for much of the Tertiary and grew under a variety of environmental conditions.

Family *incertae sedis*

? cycad

Specimens examined. C-257, 258, 384, 455, 458, 662

Description. With some variations in size and shape and vein number, the specimens consist of leaves with semi-opposite or alternately placed decurrent pinnae or lobes (Figs 6e-h). The near triangular lobes are usually curved upward and decrease in size toward the base but are typically about 8 mm long with a 4 mm long attachment laterally to the prominent rachis. Specimens C-258 (Fig. 6e) and C-458 have short petioles about 3 mm long. Approximately 7-15 equally spaced veins per lobe arise from the rachis, and some dichotomise near their origin. A vein anastomosis is observable on a lobe of C-347 (Fig. 6h). The veins typically run parallel toward the margin where they appear to curve upward and merge toward the segment apex.

Discussion. These specimens fall within the range of variation of the specimens from Vegetable Creek described by Ettingshausen (1888) as the Bennettitalean *Anomozamites muelleri*, although as outlined below this diagnosis is now invalid. Photographs of the Vegetable Creek specimens taken by R. S. Hill in 1986 have been examined and the Cethana specimens cannot be separated on details of morphology and venation. I have no doubt that specimen F 51336 (Fig. 6i) which was assigned to Ettingshausen's *Dryandra praeformosa* is in fact his *Anomozamites muelleri*. Although not discernable because of the quality of the photographs of the other specimens, and not recognised by Ettingshausen in his diagnosis of *A. muelleri*, this specimen clearly has some veins which dichotomise near the rachis. This taxon is obviously in need of revision. Ettingshausen referred "this most remarkable plant" to *Anomozamites*, a Bennettitalean genus which ranges from the Upper Triassic to the

Lower Cretaceous in the northern Hemisphere (Harris 1969). Harris emended the original diagnosis of the genus by Schimper and it includes the presence of cuticle. Ettingshausen did have some reservations about assigning the Vegetable Creek specimens to *Anomozamites* because the pinnae and nerves are not perpendicular to the rachis. Subsequent authors (e.g. Hollick 1932; Horiuchi and Kimura 1987) have viewed the determination with some suspicion, although Hollick is probably correct in conceding that it may have represented an insular genus "which can not be satisfactorily compared" with any extant cycads. Clearly, the true affinities of this taxon can only be ascertained when cuticle-bearing specimens are recovered. Nevertheless, the fact that the Cethana specimens belong to the same taxon is significant in itself for biogeographic reasons and for its relevance to palaeofloristic and climatic interpretations.

Order Coniferales

Family Araucariaceae

Numerous macrofossils referable to both genera in the family, *Araucaria* and *Agathis*, occur at Cethana. These include reproductive and foliar organs, and the former are described and discussed first.

Three female sporophylls have been recovered. In the Araucariaceae these structures are readily distinguishable. In *Araucaria* the seed coat is integrally fused to the cone-scale which usually has membranous wings, whereas in *Agathis* the seed coat is independent (Cookson and Duigan 1951; Hyland 1977; de Laubenfels 1988). Cone-scales of *Agathis* have a blunt apical margin or in some species a projecting flattened 'beak' whereas those of *Araucaria* have a protruding terminal spine. In *Araucaria* the apical tip of the ovuliferous scale forms a free ligule. *Araucaria* sections *Columbea* and *Intermedia* and *A.bidwillii* Hook. also have much larger cone-scale complexes (Wilde and Eames 1952). The Cethana specimens conform in all respects to *Agathis*.

Pollen cones referable to the Araucariaceae have also been recovered from Cethana. Specimen C-647 is a curved cone 37 mm long and about 10 mm wide which

tapers to a quite blunt apex (Fig. 7a). It is shortly pedunculate and subtended by several acute bracts, each about 5 mm long and 3 mm broad at the base. There are presumably well over 100 spirally placed sporophylls (about 40 are discernable on each side of the cone). Each occurs on a narrow stalk about 3 mm long, the apex apparently extending into a triangular flat apical part. This cone is of similar size to that of several species of *Agathis* and *Araucaria* section *Eutacta*, as described by Cookson and Duigan (1951), Hyland (1977) and de Laubenfels (1972, 1988).

As there is some doubt as to the generic identity of the fossil pollen cone only *Agathis* cone-scales are described as follows.

Agathis Salisbury

Agathis sp.

Specimens examined. C-223, 441, 529

Description. The dimensions of these seed cone bracts (or cone-scales) range from 22-31 mm wide x 17-22 mm long. They have a blunt, thickened distal region which is reflexed in relation to the proximal portions. C-529 is illustrated in Fig. 7b.

Discussion. Whitmore (1980) considers *Agathis* cone-scale size and to some degree shape to be variable in different parts of the cone and in cones of different degrees of maturity, and therefore regards female components to be of little taxonomic use. However, since the three fossil specimens are morphologically almost identical it is considered likely that they were derived from the equatorial region of mature *Agathis* cones of the same species. In contrast to Whitmore, in the most recent account of the genus de Laubenfels (1988) considers cone-scale (and microsporophyll) characters to be diagnostic at the subgeneric level. In his classification a group of three species, found in Malesia, New Caledonia and New Zealand (section *Rostrata*) possess the projecting 'beak'. The degree of scalloping at the base of the scales is also considered useful at the specific level. It is notable that Bigwood and Hill (1985) found a great difference between the stomatal orientations of *A. australis* (D. Don) Salisb. and *A. ovata* Warb., the two species in de Laubenfels' section *Rostrata* that they examined. This suggests that the taxonomy of *Agathis* may

Figure 7. Araucariaceae

a. Pollen cone (C-647). Scale: 10 mm. (p. 36)

b. *Agathis* cone-scale (C-529). Scale: 10 mm. (p. 37)

Figs c-e. *Araucaria* sp. 1 (C-632). (p. 38)

c. Leaf showing the rounded apex (top) and incurved base. Scale: 1 mm.

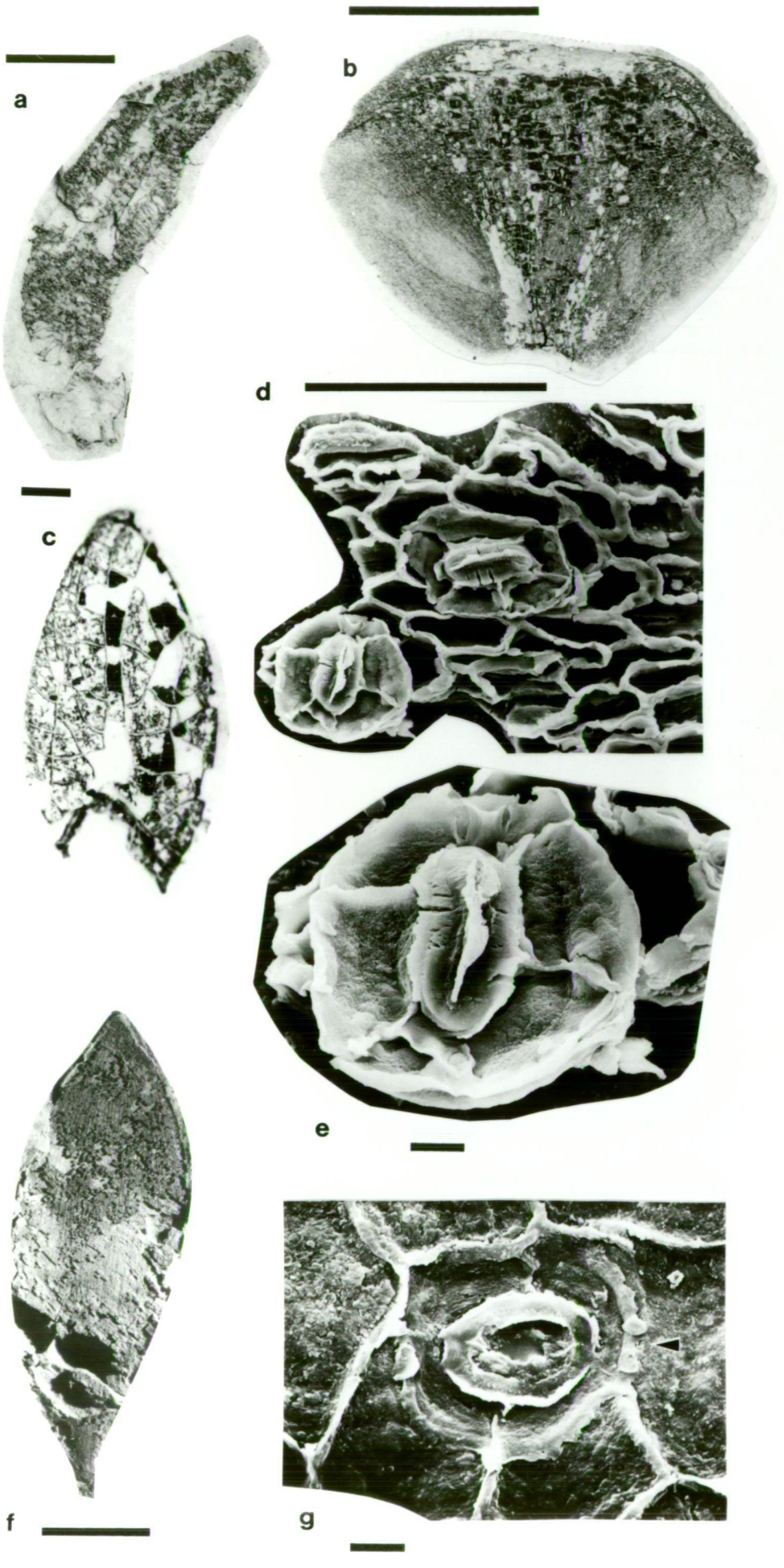
d. SEM of inner cuticle surface, showing random stomatal alignment. Scale: 10 μm.

e. SEM of single stomate showing micromorphological detail. Scale: 10 μm.

Figs f, g. *Agathis* sp. 1 (C-478). (p. 40)

f. Leaf. Scale: 10 mm.

g. SEM of stomate showing polar knobs of cuticle (arrowed). Scale: 10 μm.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still not be satisfactorily resolved.

Examination of descriptions (Hyland 1977; de Laubenfels 1972, 1978, 1988; Whitmore 1980) of mature *Agathis* cone-scales from the other two sections indicates that the Cethana specimens are most similar in size and morphology to those of several species from Malesia, Australia and New Caledonia.

Several leaves of *Agathis* and leaves and shoots of *Araucaria* have also been recognised. Taxonomically useful characters which may be used to distinguish *Agathis* from *Araucaria* are the broad leaf shape and distinct petiole, generally oblique or transverse stomatal orientation and the presence of a Florin ring associated with the stomatal apparatus in the former (Cookson and Duigan 1951; Stockey and Taylor 1981; Bigwood and Hill 1985; Hill and Bigwood 1987). There are only a few extant *Araucaria* species (in Section *Eutacta*) which have a similar stomatal orientation and in these the leaves are quite small with a broad attachment zone at the base. There are other cuticular micromorphological details which are also distinctive. Page (1980) used the SEM to study *Agathis* leaf surfaces. Many species show obvious undulations and furrows which indicate the outlines of the underlying cells. In contrast, the outer cuticle surfaces of *Araucaria* species are basically smooth (Stockey and Ko 1986). Some *Agathis* species also display distinctive knob-like thickenings at the poles of the guard cells (Stockey and Taylor 1981). However, it is not clear how much variation occurs in some of these characters, and it may be that it is considerable.

In any event, foliage of at least two species of each of *Araucaria* and *Agathis* occur at Cethana, and four species are described as follows.

Araucaria de Jussieu

Araucaria section ***Eutacta*** (Link) Endlicher

Araucaria sp. 1

Specimens examined. C-021, 546, 632, 642, 643

Description. All specimens are isolated leaves, one of which (C-632) has preserved cuticle (Fig. 7c). Leaf dimensions range from 8-17 x 4-9 mm. Their

incurved base, almost as wide as the widest point, indicates that they were probably broadly imbricate. The smoothly curved impressions in the sediment indicate they were thick with a concave adaxial surface without a marked keel. Leaf apices are rounded and the margin thickened. Numerous stomatal rows occur across the adaxial surface and the stomates, although randomly oriented (Fig. 7d), occur mostly perpendicular or oblique to the long axis of the leaf. The stomatal apparatus usually has four or sometimes five subsidiary cells and pronounced polar cuticular extensions (Fig. 7e). Florin rings are indistinct or absent.

Discussion. The gross leaf morphology and stomatal arrangement of this taxon are entirely consistent with species of *Araucaria* section *Eutacta* from New Caledonia. de Laubenfels (1972) recognised 13 species of this section from New Caledonia and there is one in Australia and New Guinea (*A. cunninghamii* D. Don) and one on Norfolk Island (*A. heterophylla* [Salisb.] Franco). The leaf dimensions of the fossils most closely resemble *A. laubenfelsii* Corbass., *A. montana* Brongn. and *A. rulei* F. Muell. The leaves of many *Araucaria* species, including *A. cunninghamii* and *A. heterophylla* are needle-like or narrow and most have an acute pointed apex. However, a rounded apex is present in *A. montana*. Stockey and Ko (1986) examined the cuticle micromorphology of all species of *Araucaria* and found that there are several features which can be used to distinguish the sections and species. As found by other workers (Cookson and Duigan 1951; Bigwood and Hill 1985) the stomatal orientation in section *Eutacta* is usually oblique or sometimes perpendicular to the long axis of the leaf whereas in the other sections (*Bunya*, *Columbea* and *Intermedia*) it is parallel. Polar extensions (of variable morphology) are mostly restricted to section *Eutacta*, particularly the smaller-leaved species. The subsidiary cell surfaces of this section are usually slightly pitted. The stomates of the fossil are mostly oriented oblique to the long axis and they have distinct polar extensions of cuticle and obvious pitting. This taxon can therefore be placed in section *Eutacta* with confidence. Although the fossils have very similar gross morphology to *A. montana*, the stomates of this species have very small polar extensions, whereas those of the fossil cuticle are pronounced. Selling (1950), Cookson and Duigan (1951), Hill and

Bigwood (1987) and Hill (1990c) have described six other *Araucaria* section *Eutacta* species with organic preservation from the Tertiary of south-eastern Australia, so it is clear that this section was diverse and widespread there during that time. The Cethana taxon is clearly distinct from these species, as they all have much smaller, usually more needle-like, falcate or prominently keeled foliage.

At least one other species of *Araucaria* section *Eutacta* occurs in the Cethana sediments. Specimens have been recovered with small spirally placed imbricate spine-like leaves, with many stomata aligned at right angles. However, these await further study.

Agathis sp.1

Specimen examined. C-478

Description. The leaf is lanceolate, 43 mm long and 15 mm wide (Fig. 7f). The base tapers to a broad petiole and the apex is acuminate. There are about 15 parallel veins. The leaf surface is quite smooth with indistinct Florin rings. Stomates are apparently restricted to numerous discontinuous rows on the abaxial surface. Their orientation is variable, but most (over 50%) are longitudinal or slightly oblique (0-40°) to the long axis of the leaf (n=90). Guard cells are sunken below subsidiary cells. There are usually four subsidiary cells or rarely five. Polar extensions of cuticle extend underneath the surrounding epidermis with two knobs of cuticle (polar knobs) sometimes visible at each end (Fig. 7g).

Agathis sp. 2

Specimen examined. C-489

Description. This leaf is linear, petiolate, tapering to the apical end and up to about 75 mm long (lacking apex) and only 6 mm wide. The leaf margin is entire and about 10 parallel veins are visible. The leaf surface has prominent cell outlines which are raised higher than the Florin rings (Fig. 8a). There are a few adaxial stomates, but most occur on the abaxial surface in discontinuous rows. Stomatal orientation is variable, but most (over 50%) are perpendicular or highly oblique to the long axis of

Figure 8. *Agathis*

Figs a-c. *Agathis* sp. 2 (C-489) cuticle. (p. 40)

a. SEM of outer abaxial surface showing prominent surface sculpture. Scale: 100 µm.

b. SEM of inner abaxial surface showing alignment of stomates more or less at right angles to the long axis of the leaf. Scale: 100 µm.

c. SEM of stomate showing lack of polar knobs. Scale: 10 µm.

Figs d, e. *Agathis* sp. 3 (C-534) cuticle. (p. 41)

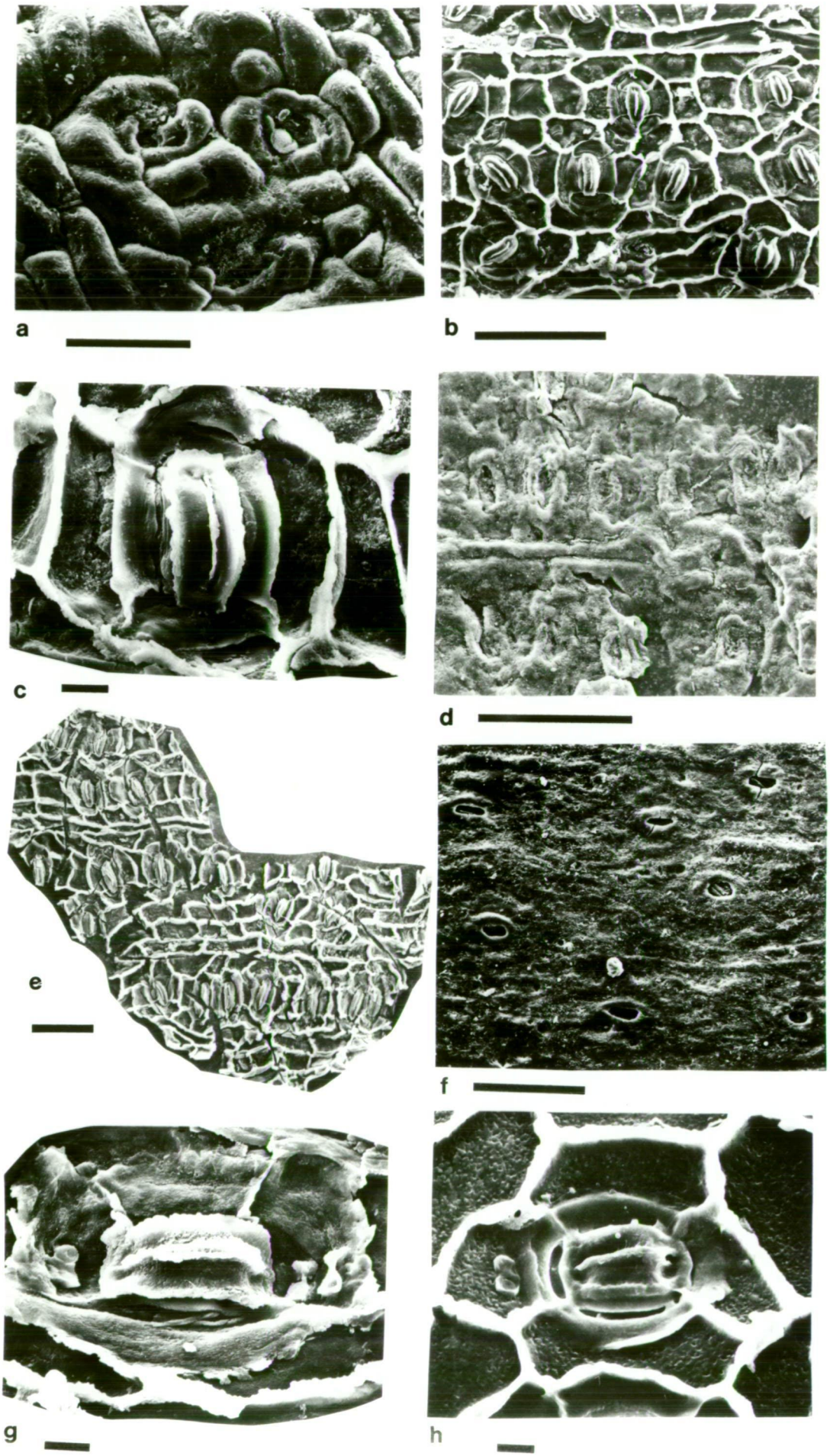
d. SEM of outer abaxial surface showing Florin rings. Scale: 100 µm.

e. SEM of inner abaxial surface showing alignment of stomates. Scale: 100 µm.

f. C-468. SEM of outer abaxial cuticle surface. Scale: 100 µm.

g. C-491. SEM of stomate showing polar knobs. Scale: 10 µm.

h. Extant *Agathis robusta.* SEM of stomate showing polar knobs. Scale: 10 µm.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the leaf (60-90°) (Fig. 8b). There is no evidence for the presence of polar knobs on any of the 180 stomates examined (Fig. 8b,c). There are usually four but sometimes five subsidiary cells.

Agathis sp. 3

Specimen examined. C-534

Description. This is an incomplete petiolate leaf (lacking apex) 8 mm wide and estimated to be 50 mm long. About 14 parallel veins are visible. The leaf surface is relatively smooth but there are distinctive Florin rings (Fig. 8d). The leaf is apparently hypostomatic, the stomates usually aligned perpendicular to the long axis of the leaf (Fig. 8d, e) (88% of the 70 stomates examined were aligned at 60-90°). Polar knobs were observed on only a few stomates.

***Discussion of* Agathis.** According to existing understanding of *Agathis* cuticles specific status must be given to each of the three taxa described above. Several other specimens from Cethana have at least some combination of characteristics which allow them to be assigned to *Agathis* with confidence, but it is considered that a thorough revision of leaf and cuticular characters in the extant species is needed (similar to the study of *Araucaria* by Stockey and Ko [1986]) before precise taxonomic conclusions can be drawn. In fact, as I have indicated, the taxonomic relationships of extant *Agathis* species seem to be unclear, and it may be that, at least in terms of cuticular characters, there is more variation within individual species and less between them than currently recognised. Data highlighting the variation of the Cethana *Agathis* leaves is presented on the following page (table 4.1). Only those specimens for which more than 30 stomates were examined are included.

Table 4.1. Cuticular details for *Agathis* specimens.

specimen	stomatal alignment %			no. of stomates	surface	polar knobs
	0-30°	31-60°	61-90°	examined	ornamentation	
C-478 sp.1	54	36	10	90	no	yes
C-489 sp.2	13	25	62	180	yes	no
C-534 sp.3	4	8	88	70	no	yes
C-468	43	32	25	138	no	yes
C-491	44	36	20	114	yes	few
C-484	24	39	37	68	no	no
C-622	14	30	56	50	no	no

From this table it could be argued that the *Agathis* leaves so far recovered from Cethana belong to at least five species. This is ecologically (and taphonomically) unlikely, although aside from possible differences attributable to differential preservation there are obvious variations in stomatal alignment, surface ornamentation, the presence of polar knobs and distribution of stomates. Specimen C-468 has a relatively smooth leaf surface (Fig. 8f) and may be conspecific with species 1, but the polar knobs are much more frequent. C-491 has excellently preserved cuticle and may be conspecific with species 2 since it has an obviously ornate surface. However, its stomatal orientation is quite random and polar knobs have been observed on some stomates (Fig. 8g). Hill and Bigwood (1987) described the first species of *Agathis* recorded from Tasmania, *A. tasmanica*, from Little Rapid River. It has a predominantly oblique stomatal arrangement (usually 40-80°). Although it is not discussed by the authors *A. tasmanica* possesses stomatal polar knobs (Hill and Bigwood 1987; their Fig. 4J). Thus, it is unlikely that it is closely related to *A. moorei* (Lindl.) Masters and *A. corbassonii* de Laub., the extant species considered by Hill and Bigwood to be most similar to this fossil, since these species apparently lack the knob-like thickenings (Stockey and Taylor 1981). A stomate of the Queensland species *A. robusta* (C. Moore ex F. Muell.) Bailey showing the polar knobs is illustrated in Fig. 8h.

Agathis now occurs in New Zealand, Queensland, Malesia, Fiji, Vanuatu and New Caledonia, where it has been recorded in a variety of lowland to montane rainforest types.

Family Cupressaceae

Papuacedrus Li

Papuacedrus australis R. Hill & Carpenter

Specimens examined. C-225, 234, 259, 349

This species were described and discussed by Hill and Carpenter (1989-appendix II).

Libocedrus Endlicher

Libocedrus morrisonii R. Hill & Carpenter

Specimen examined. C-553

Description. The specimen exists as a branched shoot with opposite pairs of leaves (Fig. 9a). The lateral leaves are free, up to 2.5 mm long and 0.6 mm wide, and have an acute apex. They are frequently of similar length to the facial leaves. Stomatal distribution is indeterminable. Stomates with lobed Florin rings (Fig. 9b) are found in zones which are generally free of papillae. Papillae are abundant in the non-stomatal regions.

Discussion. Hill and Carpenter (1989-appendix II) also discussed this species from the Oligocene Pioneer deposit. The Cethana fossil is assigned to *L. morrisonii* since its macromorphological and cuticular features match those of this species. Most diagnostic is the apparent rarity of the distinctive cupressaceous papillae in the stomatal regions, and the fact that the facial leaves are relatively long.

Family Podocarpaceae

Acmopyle Pilger

Acmopyle glabra R. Hill & Carpenter, sp. nov.

Specimens examined. C-222, 226

Hill and Carpenter (1991-appendix I) recognised the presence of *Acmopyle* foliage at Cethana and several other south-eastern Australian deposits. C-226 is illustrated (Fig. 9c) as it was not figured in the paper.

Figure 9.

Figs a, b. *Libocedrus morrisonii* (C-553). (p. 43)

a. Section of shoot. There are opposite pairs of lateral and facial leaves. Scale: 1 mm.

b. SEM of outer abaxial cuticle surface showing a lobed Florin ring (arrowed left) and a papilla (arrowed right). Scale: 10 μm.

(p. 43)

c. *Acmopyle glabra* (C-226). Non cuticle-bearing shoot. Scale: 10 mm.

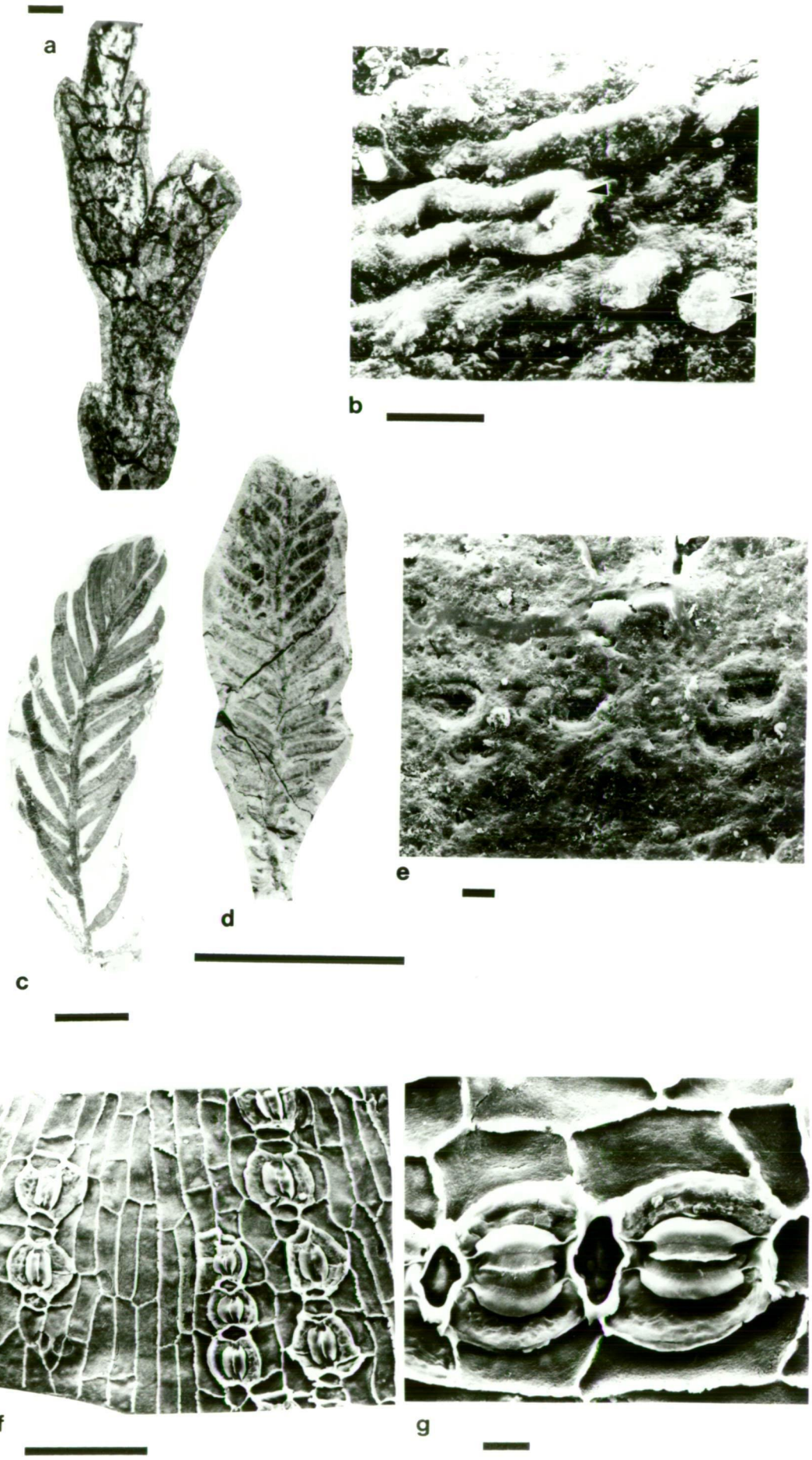
Figs d-g. *Dacrycarpus falcatus*. (p. 44)

d. C-203. Non cuticle-bearing shoot. Scale: 10 mm.

e. C-619. SEM of outer cuticle surface showing indistinct Florin rings. Scale: 10 μm.

f. C-619. SEM of inner abaxial cuticle surface showing rows of stomates. Scale: 100 μm.

g. C-619. Enlargement of two stomates shown in **Fig. 9f.** Scale: 10 μm.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Dacrycarpus (Endl.) de Laubenf.

Dacrycarpus falcatus Wells & R. Hill

Specimens examined. C-052, 203, 619

These bilaterally flattened specimens were assigned to *D. falcatus* by Hill and Carpenter (1991) and a copy of this paper is provided in the appendix. Specimen C-203 (a short shoot) and cuticle from C-219 are illustrated (Figs 9d-g), as the Cethana specimens were not figured in this paper.

Dacrydium Soland. ex Lamb.

Dacrydium sp. 1

Specimens examined. C-202, 471

Description. The specimens are represented by foliage shoots with spirally arranged, loosely imbricate, strongly keeled leaves up to 5 mm long and less than 1 mm wide (Fig. 10a). These leaves are often slightly curved and have an acute apex. The leaves are apparently unequally amphistomatic, with most stomates occuring on the adaxial surface, although the precise stomatal distribution is indeterminable. Poorly developed Florin rings are present. The stomates occur in discontinuous parallel rows up to four stomates wide. The epidermal cells between the rows have relatively straight anticlinal walls (Fig. 10b). Walls on the adaxial surface may be slightly buttressed, but buttressing is most noticeable on the abaxial surface (Fig. 10c). Epidermal cells are rectangular and arranged in files parallel to the long axis of the leaf. Periclinal walls are smooth. The stomatal apparatus has pronounced polar cuticular extensions (Fig. 10d) and the polar subsidiary cells may be shared between neighbouring stomates in the same row. Usually there are two polar and two lateral subsidiary cells but sometimes the latter are divided, giving at least four cells.

Discussion. The combination of gross morphological and cuticular characters entirely conforms to that described in detail by Wells and Hill (1989a) for *Dacrydium* and leaves no doubt that these specimens can be assigned to the genus with confidence. In particular, these authors, Florin (1931) and Stockey and Ko (1990) emphasise the diagnostic character of the highly sinuous or buttressed anticlinal cell

Figure 10. ***Dacrydium***

Figs a-d. *Dacrydium* sp. 1. (p. 44)

a. C-202. Section of shoot with spirally arranged foliage. Scale: 1 mm.

b. C-471. SEM of inner adaxial cuticular surface from the leaf apex. Scale: 100 μm.

c. C-202. SEM of inner abaxial cuticular surface showing anticlinal wall buttressing. Scale: 100 μm.

d. C-471. SEM of partially degraded stomate with one polar subsidiary cell at left. Note the polar guard cell cutin extension. Scale: 10 μm.

Figs e-i. *Dacrydium* sp. 2. (p. 45)

e. C-517. Section of shoot with spirally arranged foliage. Scale: 1 mm.

f. C-517. LM of marginal frill. Scale: 100 μm.

g. C-519. SEM of inner adaxial cuticle surface showing a band of stomates. Scale: 50 μm.

h. C-519. SEM of inner abaxial cuticle surface showing buttressing of anticlinal walls. Scale: 10 μm.

i. C-517. SEM of stomate. Scale: 10 μm.

j. Extant *Dacrydium novoguineense*. LM of marginal frill. Scale: 100 μm.

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walls, particularly on the abaxial surface. Unfortunately the stomatal distribution of the Cethana specimens was not ascertained owing to the fragmentary nature of the cuticle. However, it is clear that this species is distinct from the three species described by Wells and Hill (1989b) from other Oligocene deposits in Tasmania, since two of them have much shorter needles, and the other, *D. aciculare*, has epidermal cells with much more heavily buttressed anticlinal walls. The foliage of the Cethana specimens is very similar to that of juvenile branchlets of the Malesian species *D. elatum* (Roxb.) Wall. ex Hook. and the adult leaves of several other species described by de Laubenfels (1988). Other specimens (C-328, 370) have been recovered but lack cuticle. Specimen C-080 also lacks cuticle but may be conspecific with *D. aciculare* since it has more densely arranged, long needle-like leaves.

Dacrydium sp. 2

Specimens examined. C-517, 519

Description. These foliage shoots have imbricate, spirally arranged, strongly keeled, straight acicular leaves up to 3mm long (Fig. 10e). A distinct regular marginal frill of ctenoidal cells up to 75 μm long at the apex occurs on C-517 (Fig. 10f), but is not as well developed on C-519. The leaves are amphistomatic with the stomates on the abaxial surface being restricted to the basal third to half of the surface, where they may occur sparsely. Florin rings are present. The adaxial stomates occur in discontinuous rows two-to-five stomates wide and are typically separated by relatively straight walled epidermal cells (Fig. 10g). Outside the stomatal bands the anticlinal walls of the cells are markedly buttressed, particularly on the abaxial surface (Fig. 10h). The periclinal walls are smooth and sometimes form grooves. The stomatal apparatus is almost amphicyclic with two short polar subsidiary cells (Fig. 10i), but the lateral subsidiary cells may be divided. The polar cells are shared or abut between those of neighbouring stomates in the same row. There is a guard cell cuticular flange and polar extensions with median ridges occur. A narrow flange also occurs laterally.

Discussion. These specimens are assigned to a different species because the leaves are much shorter and more closely imbricate than those of *Dacrydium* sp. 1.

C-517 possesses an obvious marginal frill, which, according to Wells and Hill (1989a) only occurs in two of the 16 extant species, including *D. novo-guineense* Gibbs (Fig. 10j). These species both have narrow, appressed sharply keeled scale leaves, and are thus different to the Cethana species. However, in all other respects the fossils are very similar to *D. novo-guineense*, which occurs in montane New Guinea, Celebes and the Moluccas. The other species, *D. araucarioides* Brongn. & Gris. of New Caledonia, has marked anticlinal and periclinal cell wall buttressing and is thus clearly distinct from the fossils.

***Discussion of* Dacrydium.** The recognition of at least two species at Cethana is not unexpected since Wells and Hill (1989b) note that three other Oligocene deposits, including two in Tasmania, contain macrofossils of *Dacrydium* s. str. species. The genus, as recognised by Quinn (1982) is now restricted to the Malesian and south-western Pacific tropics, with the exception of *D. cupressinum* Soland. ex Lamb which occurs throughout New Zealand. The trees occur in a variety of everwet, humid rainforest types, most commonly in the montane low latitude regions. It is significant that one of the Cethana taxa has a marginal frill, and exhibits other morphological similarities to *D. novo-guineense*, which may be found near the tree-line in the mossy heath forests of New Guinea. In *Dacrydium* s.l., this frill is otherwise only found in the cold temperate species of Tasmania, New Zealand and Chile and may represent an adaptation to limit water loss in extreme environments. Many *Dacrydium* species are also characteristic of oligotrophic peat swamps and open sandy environments (Whitmore 1975; Bruenig 1987; van Steenis 1979; de Laubenfels 1988).

Lagarostrobos Quinn

Lagarostrobos sp.

Specimens examined. C-340, 540, 735

Description. These specimens are represented by stems about 2 mm in diameter with strongly keeled, spirally arranged, closely imbricate overlapping

rhomboidal scale leaves (Figs 11a, b). The apices are blunt and the leaf margins are entire with a marginal frill of regular ctenoidal cells up to 60 μm long (Fig. 11c). The cuticle is amphistomatic with randomly arranged stomata which have four to six amphicyclic subsidiary cells (Figs 11d, e). Florin rings are pronounced and sunken to the level of the leaf surface (Fig. 11f). Resin plugs removed from under the leaf keels indicate the presence of resin canals below the vascular traces. The epidermal periclinal walls are smooth and there is no noticeable beading or buttressing of the anticlinal walls (Fig. 11g).

Discussion. Living conifers possessing spirally arranged closely appressed imbricate scale leaves are the imbricate Podocarpaceae (especially *Microstrobos*, some species of *Dacrydium* s. str. and *Dacrydium* Group C) and *Athrotaxis cupressoides* D. Don (Offler 1984). Townrow (1965b) described specimens with a much narrower stem axis and smaller leaves than *A. cupressoides* from the Early Tertiary in Tasmania as *A. ungeri*. Unfortunately these specimens are no longer available for study, but Townrow noted that the genus possesses distinctive morphological and cuticular features which clearly separate it from the fossil described here. Most notably these are a lack of a distinct leaf keel, the presence of a collar around the stomatal pit and a marginal fringe made up of non-uniform cells with finger-like projections. *Microstrobos* has stomates arranged in files parallel to the long axis of the leaf with elongate epidermal cells (Wells and Hill 1989a), and is thus also clearly different from the fossils.

Quinn (1982) split *Dacrydium* Group C (Florin 1931) into *Halocarpus* (New Zealand), *Lagarostrobos* (Tasmania, New Zealand), and *Lepidothamnus* (New Zealand, Chile) on the basis of cone structure. Recent SEM cuticular studies by Wells and Hill (1989a, 1989b) support this taxonomy. However, these authors note that the cuticles of the two species of *Lagarostrobos* are quite distinct and that this supports the evidence of other authors who suggest that these species should not be placed in the same genus. Nevertheless, the group can easily be separated from other imbricate Podocarpaceae including some species of *Dacrydium* s. str. and *Microstrobos* in having randomly oriented, isolated, regularly shaped amphicyclic stomata, with

Figure 11. ***Lagarostrobos*** (p. 46)

Figs a-c. C-340.

a. Section of stem. Scale: 1 mm.

b. Drawing of stem section to show spirally placed imbricate leaves. Scale: 1 mm.

c. LM of marginal frill. Scale: 50 µm.

Figs d, e. C-540 cuticle.

d. SEM of inner surface showing randomly aligned stomates. Scale: 100 µm.

e. Enlargement of two stomates shown in **Fig. 11d.** Scale: 10 µm.

f. C-525. SEM of outer surface showing a prominent Florin ring. Scale: 10 µm.

g. C-340. SEM of inner cuticle surface showing relatively smooth epidermal walls. Scale: 10 µm.

h. Extant *Lagarostrobos colensoi*. LM of marginal frill. Scale: 50 µm.


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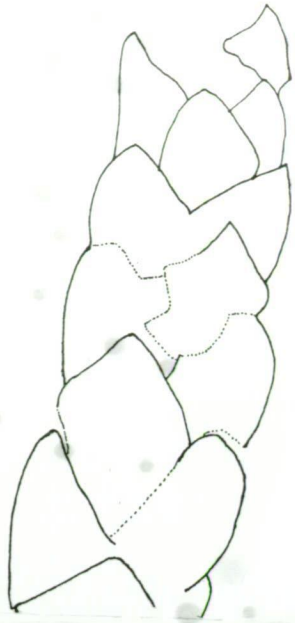
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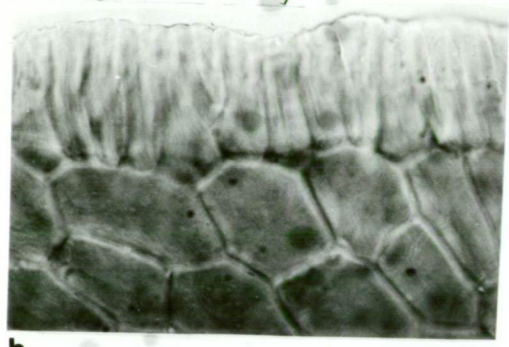
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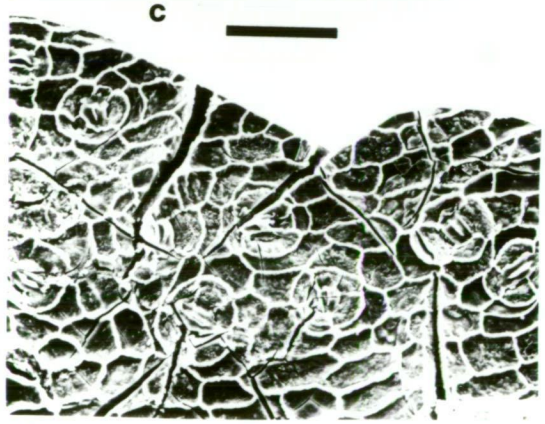
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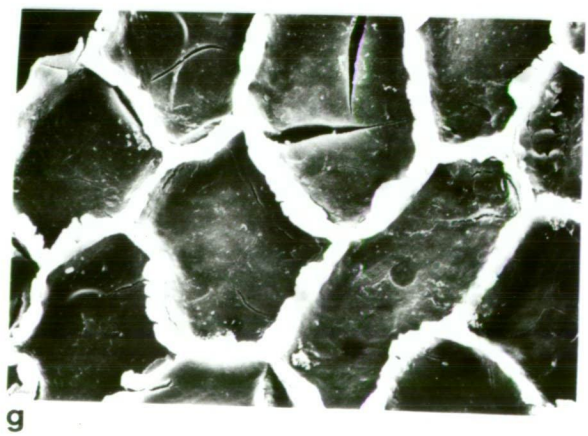
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random orientation of polygonal epidermal cells. In vegetative characters, *Lepidothamnus* can be separated from *Halocarpus* and *Lagarostrobos* in having more spreading foliage, distinctly U-shaped periclinal cell walls (Wells and Hill 1989a) and an absence of resin canals (Quinn 1982; Tengner 1965). The Cethana fossils are distinct in all of these features, and are therefore not *Lepidothamnus*. There are two extant species of *Lagarostobos*, *L. franklinii* (Tasmania) and *L. colensoi* (Hook.) Quinn (New Zealand) and Wells and Hill (1989b) assigned a single fossil from the Oligocene Little Rapid River deposit of Tasmania to a new species, *L. marginatus*. However, this specimen completely lacks a marginal frill, a character common to all other Group C *Dacrydium* species, and therefore this generic determination may not be tenable. However, a significant result from their study was that Wells and Hill (1989a) found that the cuticle of *L. colensoi* is very similar to that of *Halocarpus*, particularly *H. kirkii* (F. Muell. ex Parl.) Quinn. Therefore, in the absence of reproductive organs, it is difficult to be certain of the affinity of the Cethana specimens, although it should be stressed that an affinity to these taxa is far clearer than the generic determination of *Lagarostobos* proposed by Wells and Hill (1989b) for their specimen. The morphology and length of the uniform marginal frill of the Cethana specimens is similar to that of *L. colensoi* (Fig. 11h), *H. bidwillii* (Hook. f. ex T. Kirk) Quinn and *H. biformis* (Hook.) Quinn, but shorter than that of *H. kirkii*. The micromorphology of the stomatal apparatus of these species is very similar, but the lack of any buttressing or beading of the anticlinal cell walls indicates affinity to *Lagarostrobos*, and on this basis the fossils are assigned to that genus. The three extant species of *Halocarpus* and *L. colensoi* are restricted to New Zealand, where they typically occupy a range of very wet habitats, including montane bogs (Salmon 1980).

Phyllocladus L. C. & A. Rich

Phyllocladus sp. 1

Specimen examined. C-305

Description. The specimen is 29.5 mm long with numerous relatively long,

narrow lobes (max. width 2.9 mm) which are up to at least 17 mm long (Fig. 12a).

Phyllocladus sp. 2

Specimen examined. C-352

Description. This specimen is represented by segments of a compound phylloclade or shoot with four phylloclades (Fig. 12b). These are up to 19 mm long and 8 mm wide.

***Discussion of* Phyllocladus.** Hill (1989a) recently described and discussed *Phyllocladus* macrofossils from south-eastern Australia. Although both of the Cethana specimens can be referred to the genus with confidence because of their distinctive lobed shoot morphology with reduced scale leaves and dichotomising veins in their phylloclades, there is unsufficient evidence to be certain of their affinities since cuticular preservation is lacking. In the Oligocene Little Rapid River deposit Hill recognised two types of phylloclade morphology and was able to demonstrate that their cuticles were also distinct. Hence, he designated specific rank to the two taxa. Species 1 from Cethana may be conspecific with *P. lobatus* since it possesses the relatively long, narrow segments diagnostic for this taxon (Hill 1989a). *Phyllocladus lobatus* was shown by Hill to have no close affinity to the extant species. Species 2 is more similar to other fossil and extant species, such as *P. hypophyllus* Hook. f. from Malesia. The genus is now restricted to Tasmania, New Zealand and Malesia. In New Guinea it is characteristic of montane rainforests.

Podocarpus L' Herit. ex Persoon

subgenus *Podocarpus* de Laubenfels

Podocarpus sp. 1

Specimen examined. C-610

Description. The single entire-margined leaf is incomplete at the base and apex although tapering to the basal end suggests an estimated length of at least 40 mm. Its maximum width is about 5 mm and a midvein 1mm wide is also visible. The stomates occur in two distinct broad bands up to at least 10 rows wide either side of

Figure 12.

a. Phylloclade of *Phyllocladus* sp. 1 (C-305). Scale: 10 mm. (p. 48)

b. Phylloclade(s) of *Phyllocladus* sp. 2 (C-352). Scale: 10 mm. (p. 49)

Figs c, d. *Podocarpus* sp. 1 (C-610) cuticle. (p. 49)

c. SEM of inner abaxial surface showing files of stomates in part of a stomatal band. Scale: 100 μm.

d. SEM of outer abaxial surface showing Florin rings. Scale: 10 μm.

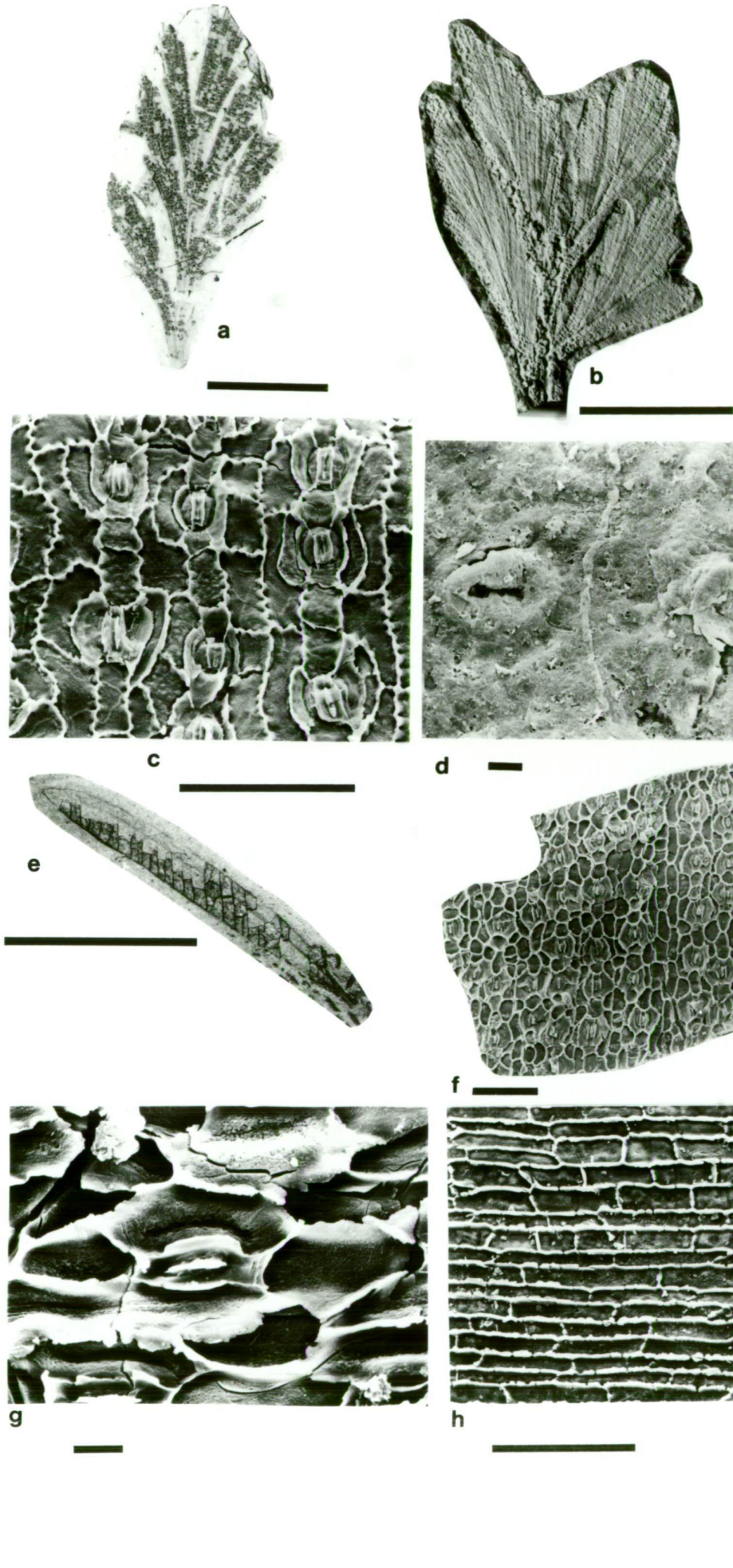
Figs e-h. *Podocarpus* sp. 2. (p. 51)

e. C-275. Isolated leaf with twisted leaf base. Scale: 10 μm.

f. C-275. SEM of inner abaxial cuticle surface showing a band of stomates. Scale: 100 μm.

g. C-274. SEM of stomate. Scale: 10 μm.

h. C-275. SEM of inner adaxial cuticle surface. Scale: 100 μm.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the midvein (Fig. 12c). They are apparently restricted to the abaxial surface and have quite distinct Florin rings (Fig. 12d). Up to three rows of elongate epidermal cells may occur between the stomatal rows. The stomates usually have two polar and two lateral subsidiary cells and are paratetracytic (Fig. 12c). The polar cells are usually elongate rectangles extending well beyond the apices of the crescentic subsidiary cells. The cuticular flange between guard cells and subsidiary cells has pronounced polar extensions and the stomatal pore is rectangular. The marginal and venous epidermal cells are elongate rectangles. The epidermal cells on the adaxial surface are typically squares or short rectangles and are arranged in uniform files, often with their long axes perpendicular to the long axis of the leaf. The anticlinal walls of the epidermal cells are buttressed so as to give the cuticle a sinuous appearance (Fig. 12c).

Discussion. Page (1988) recently proposed taxonomic alterations in the Podocarpaceae with broad leaves, and these are accepted here. Taxa with broad leaves which are not falcate and arranged distichously in short shoots are *Podocarpus*, *Prumnopitys*, *Saxegothea conspicua* Lindl., *Sundacarpus amara* (Blume) C. N. Page (formerly *Prumnopitys amara* [Blume] de Laub.), *Nageia*, *Retrophyllum* (formerly *Nageia* sect. *Polypodiopsis*) and *Afrocarpus* (formerly *Nageia* sect. *Afrocarpus*). Of these, *Nageia* differs from all other Podocarpaceae in having multiveined leaves and *Prumnopitys*, *Sundacarpus*, *Retrophyllum* and *Afrocarpus* can readily be distinguished from *Podocarpus* on epidermal characteristics (e.g. Florin 1931; Greenwood 1987a; Stockey and Ko 1988; Hill, Carpenter, unpublished). In particular, although the anticlinal cell walls of *Podocarpus* may be beaded, slightly sinuous or buttressed they are never as heavily buttressed or as sinuous as most species of *Prumnopitys*. In contrast to those of *Podocarpus*, the stomates of *Prumnopitys* are typically amphicyclic, since the polar subsidiary cells are small and tend to be at least partially surrounded by the lateral subsidiary cells. Also, the polar subsidiary cells are rarely, if ever shared between consecutive stomates in a row. The rows themselves are very indistinct and in most species therefore tend to cover most of the leaf surface. In *Podocarpus* distinct stomatal rows are found in discrete bands either side of a wide stomate free zone over the midvein (Greenwood 1987a). This

situation also occurs in the Chilean genus *Saxegothea*, but the stomates have obvious micromorphological differences to those of *Podocarpus*. In addition, there is no evidence that *Saxegothea* has ever occurred outside Chile (Florin 1963).

According to de Laubenfels (1988) there are 95 species of *Podocarpus* in two subgenera. The potential for cuticular characters to be used in the infrageneric classification of *Podocarpus* is currently being explored in our laboratory.

This Cethana species can clearly be assigned to subgenus *Podocarpus*, since the species in this section have obvious Florin rings. This group is now mostly associated with the high latitude forests of Tasmania, New Zealand, and Chile but extends into the montane tropics of Africa and America (de Laubenfels 1985). Townrow (1965) and Greenwood (1987a) have described species of *Podocarpus* subgenus *Podocarpus* from Australian Eocene sediments.

subgenus ? ***Foliolatus*** de Laubenfels

Podocarpus sp. 2

Specimens examined. C-251, 274, 275, 342, 492

Description. These fossils are represented by individual linear leaves, 15-25 mm long and 2-2.8 mm wide (Fig. 12e). A short twisted petiole is present although the arrangement of the leaves on the stem is unknown. The leaf apex is pointed, but not acuminate. A single midvein trace occurs. Stomates are apparently restricted to the abaxial surface but Florin rings are indistinct. They occur in two bands either side of a wide stomate-free zone over the midvein, in non-uniform rows, typically about nine stomates wide (Fig. 12f). Stomates are usually paratetracytic, with crescentic lateral subsidiary cells and elongate polar cells which are often shared between successive stomates in a row (Fig. 12g). A flange of cuticle occurs between the guard cells and a flange also extends laterally parallel to the subsidiary cells. Prominent polar extensions also occur as well as a variably thickened flange between the subsidiary cells and adjacent epidermal cells. Epidermal cells are regularly elongate rectangles. The anticlinal walls are smooth or slightly beaded, but not sinuous (Fig. 12h).

Discussion. This species is abundant in the sediments and differs from species 1 in several aspects. The leaves are smaller and the epidermal cells differ in being more elongate and in having only slight beading and never anticlinal wall sinuosity. Further, these specimens probably belong to subgenus *Foliolatus*, since the stomates lack obvious Florin rings. Hill and Carpenter (1991-appendix I) found that a specimen from Vegetable Creek referred to *Dacrycarpus* by Ettingshausen is in fact *Podocarpus*, probably subgenus *Foliolatus*.

Coniferales *incertae sedis*

Specimens examined. C-201, 210, 510, 522, 560, 563, 728, 729, 780

Description. It is difficult to interpret the phyllotaxy of the specimens on the compression and impression fossils (Figs 13a-c), but it is clear from specimens such as C-780 that the leaves show dimorphic characteristics, probably associated with seasonal growth increments. A unique feature is the apparent flanging of the stem between pairs of leaflets, though it is conceivable that the leaf bases were decurrent and somewhat expanded. The leaves are sub-petiolate or at least highly constricted/twisted at the base, and are broadly lanceolate, straight, from 3-10 mm long and 1-4.5 mm wide. The apex is rounded and typically has an apiculate tip. A single distinct midvein is present. The leaf arrangement appears to be opposite or sub -opposite and the leaves were probably inserted in one plane. Study of C-201 using oblique lighting and low power LM demonstrates that the leaves were almost certainly distichous (leaves twisted at the base to bring the same surface uppermost on both sides of the stem) since the impressions of papillae and stomates are visible on leaves on each side of the stem axis. The cuticle, though fragmentary, is well preserved, and allows quite detailed micromorphological features to be determined. Stomates are restricted to the abaxial leaf surface, in distinct zones at least three stomates wide, either side of the midvein. They occur in long discontinuous files from base to apex, parallel to the long axis of the leaf, often separated by up to three rows of epidermal cells. Under LM the anticlinal walls of these cells are difficult to distinguish as their

Figure 13. Unknown conifer (p. 52)

a. C-728. Section of shoot showing leaf arrangement and flanged stem. Scale: 10 mm.

b. C-201. Section of shoot. Scale: 10 mm.

c. C-510. Section of shoot showing shortly petiolate leaves which have become detached from the stem axis. Scale: 1 mm.

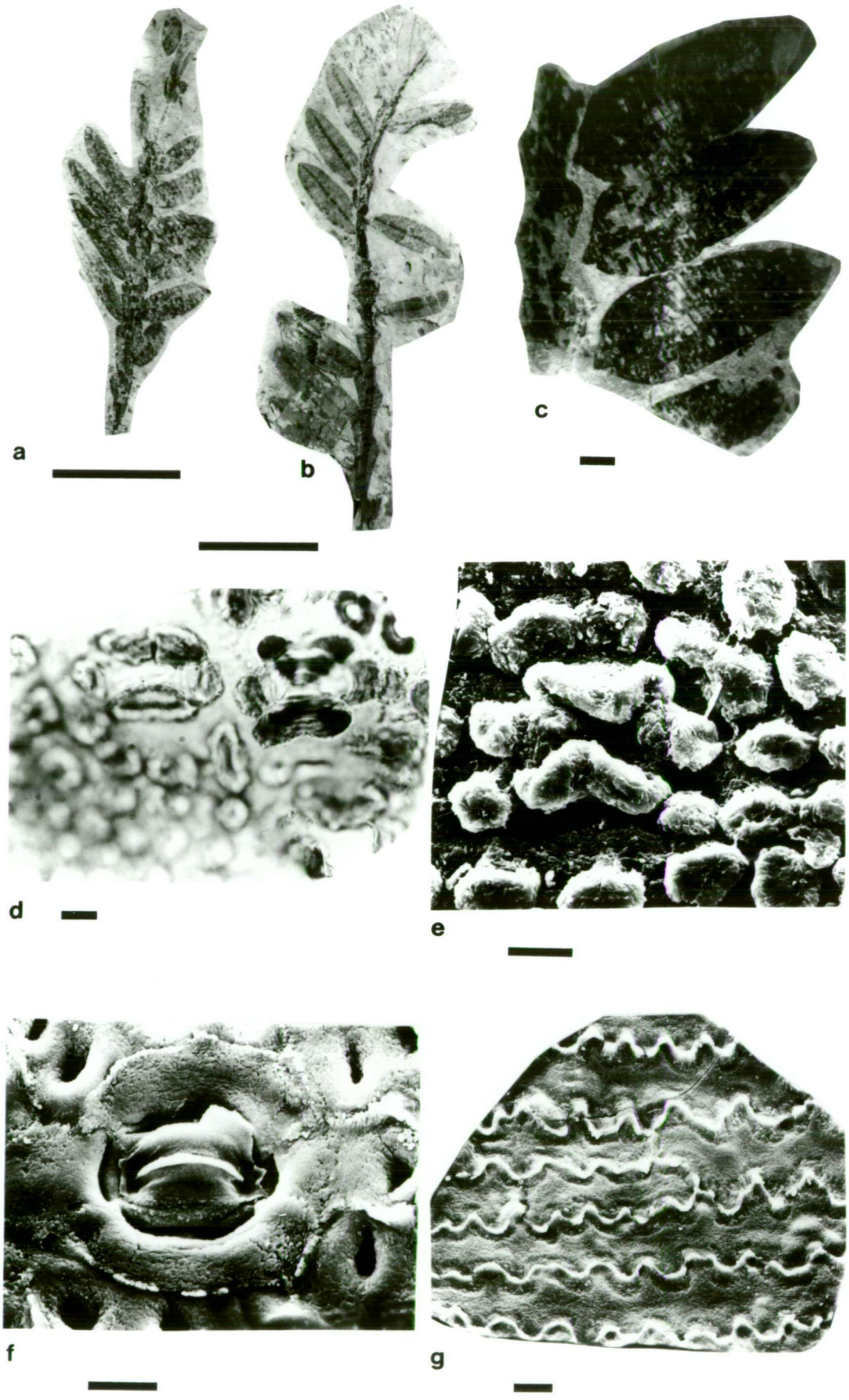
Figs d-g. C-522 cuticle.

d. LM of abaxial side showing papillae and stomates. Scale: 10 µm.

e. SEM of outer abaxial surface. Scale: 10 µm.

f. SEM of stomate. Note also the prominent depressions left by the epidermal cells and which correspond to the papillae observed on the outer surface. Scale: 10 µm.

g. SEM of inner adaxial surface showing sinuous anticlinal walls. Scale: 10 µm.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straight walls are quite thin and masked by prominent donut-like papillae (Fig. 13d). Under SEM it can be seen that these are actually outgrowths of the epidermal cells and they are restricted to the stomatal regions of the abaxial surface (Fig. 13e). The stomates are typically paratetracytic, with two rectangular polar subsidiary cells and two lateral crescentic subsidiary cells (Fig. 13f). The polar cells are frequently shared between successive stomates in the rows. The guard cells have polar, and where undamaged, prominent lateral cutin extensions. The subsidiary cells and/or their papillate extensions overarch the guard cells, and frequently appear to close off the stomatal pore (Figs 13d, e). The flanged or decurrent basal regions appear similar to the leaves in terms of stomatal and papilla distribution. The outer surfaces of the epidermal cells on the adaxial surface and outside the stomatal regions on the abaxial surface are smooth. These cells are typically elongate rectangles and occur in long files. Their anticlinal walls are sinuous and not buttressed (Fig. 13g). The inner surfaces of all cells appear granular except the guard cells, which are relatively smooth.

Discussion. Several specimens of this taxon have been recovered and the distinctive cuticle has also been encountered in dispersed cuticle preparations. This taxon is of special significance in being an extinct conifer with no readily discernable fossil or extant affinity. A formal taxonomic description is pending further research, particularly comparative analysis of other extinct conifer groups including other Tasmanian Tertiary taxa. The possibility that the Cethana specimens conform most closely with conifers which supposedly became extinct in the Cretaceous is being investigated. For instance, Harris (1979) describes several species of the form genus *Elatocladus* from the Yorkshire Jurassic flora which have features in common with the Cethana fossils, such as distinctly papillose cuticles and sinuous adaxial epidermal cells. As mentioned, several remarkable Early Tertiary Tasmanian conifers are currently under investigation. For instance, Townrow (1965a) assigned coniferous shoots in the Eocene Buckland deposit to *Coronelia molinae*, a genus and species described by Florin (1940) from the Tertiary of Chile. Townrow suggested that *Coronelia* was podocarpaceous, but was uncertain because of the presence of several

unusual cuticular features such as variably developed papillae and numerous hairs in the stomatal regions and along the margins. Amongst extant gymnosperm families prominently papillose cuticles occur in members of the Cupressaceae, Taxodiaceae, Cephalotaxaceae and Taxaceae (Florin 1931). Cuticle of *Taxus baccata* L. was studied using SEM but is clearly distinct from the fossils.

4.4.3 ANGIOSPERMAE

Taxonomy follows Cronquist (1981), the system adopted for the Flora of Australia.

Order Laurales

Family Lauraceae

Laurophyllum Goeppert

Laurophyllum sp.

Specimens examined. C-479, 628

Description. Two leaves with similar architectural features to those of various genera in the family have been recovered and cuticle has been successfully prepared from one. C-479 is an entire margined elliptic leaf, 96 mm long and 33 mm wide and C-628 an elliptic-ovate leaf 100 mm long and 44 mm wide (Fig. 14a). Both leaves have acute apices and bases. The venation is eucamptodromous with about 8 prominent upcurving secondary veins. Cuticle was recovered from C-628 and the leaf is hypostomatic. The stomates are quite sparse and randomly aligned. They are paracytic with cuticular scales between the embedded guard cells and the overarching subsidiary cells (Fig. 14b). There are occasional trichome bases with a small, irregularly shaped, thickened foot cell and unmodified basal cells over and between the veins (Figs 14b, c).

Discussion. Hill (1986) briefly reviewed the fossil record of the Lauraceae and described and illustrated the distinctive characteristics of lauraceous cuticle, particularly the stomatal apparatus. He described 12 species from the Early to Middle Eocene Nerriga Flora of New South Wales but as he considered that the leaves could not be identified to generic level with confidence he placed them in the form genus

Figure 14.

Figs a-c. *Laurophyllum* sp. (C-628). (p. 54)

a. Leaf. Scale: 10 mm.

b. LM of abaxial side showing a stomate (left) and trichome base (right). Scale: 50 µm.

c. LM of adaxial side showing a trichome base. Scale: 10 µm.

Figs d, e. *Nothofagus* aff. *alessandrii* (C-457). (p. 56)

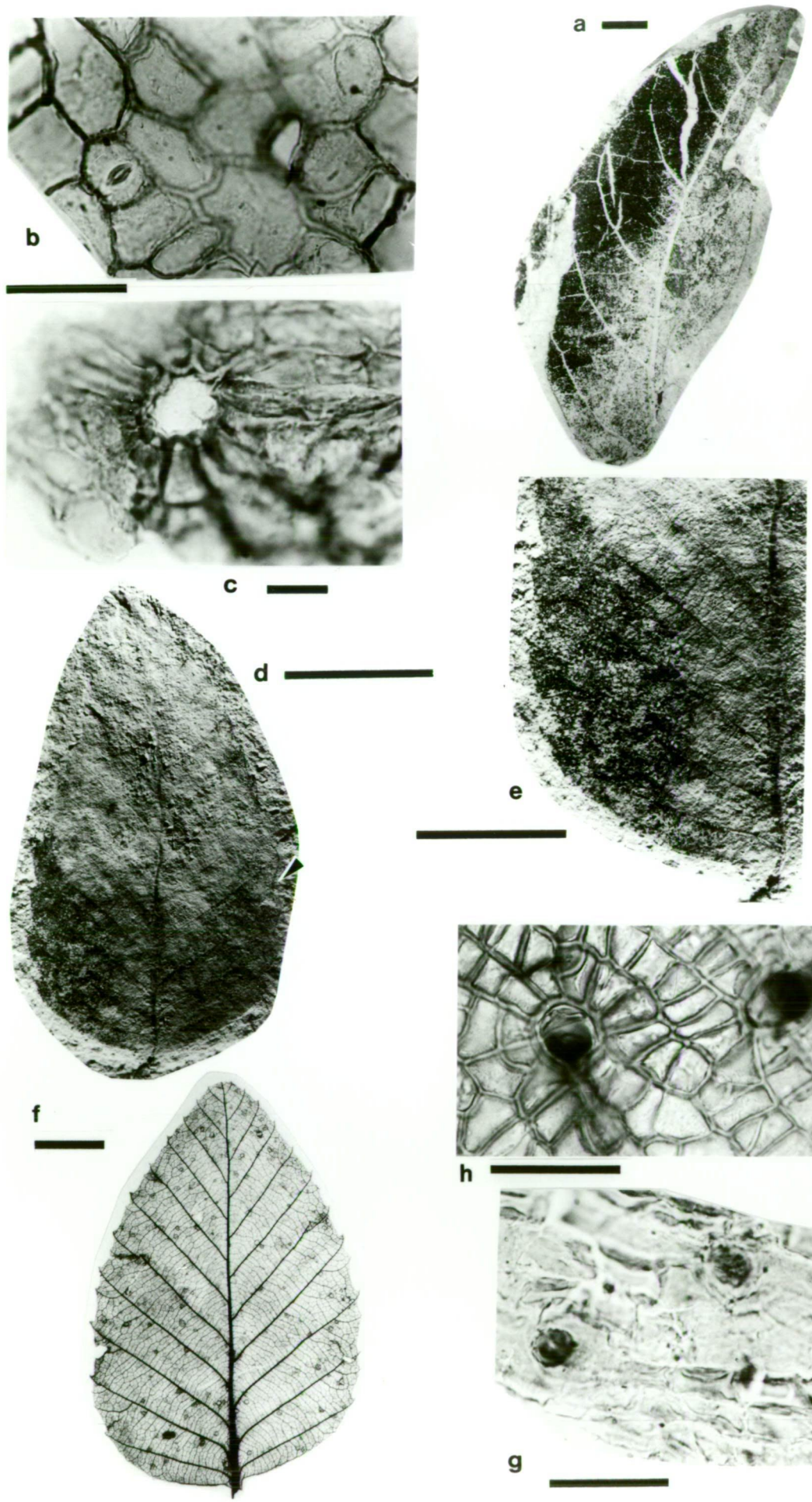
d. Leaf. Note the fimbrial vein (arrowed). Scale: 10 mm.

e. Enlargement of **Fig. 14d** showing the percurrent tertiary veins. Scale: 5 mm.

f. Cleared leaf of extant *Nothofagus alessandrii*. Scale: 10 mm.

g. LM of trichome bases on the adaxial cuticle of *Nothofagus tasmanica* (C-613). (p. 58) Scale: 50 µm.

h. LM of trichome bases on the adaxial cuticle of extant *Nothofagus moorei*. Scale: 50 µm.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Laurophyllum. The two Cethana specimens are architecturally similar to *L. arcuatum* Hill, but the cuticle of C-628 is distinct. Therefore they are considered to belong to a new species. Dispersed lauraceous cuticle fragments have also been recovered. According to Hyland (1989) there are seven genera (excluding the parasitic climber *Cassytha*) and over 100 species of Australian Lauraceae. Most species occur in rainforests of the east coast and the family is widespread globally. In contrast to Nerriga where the Lauraceae was a dominant element of the local vegetation (Hill 1986) the family was apparently not common at Cethana. Lauraceous wood (Leisman 1986) and leaves occur in many Early Tertiary fossil deposits of south-eastern Australia. They are also common in northern hemisphere Tertiary floras (e.g. Taylor 1988).

Order Fagales

Family Fagaceae

Subfamily Fagoideae

Nothofagus Blume

subgenus ***Fuscaspora*** R. Hill & Read

Nothofagus gunnii (Hook. f.) Oerst.

Discussion. Hill (1984) recorded a single specimen from Cethana which he assigned to *N. gunnii*. More recently, comparable leaves have been recovered from two relatively high altitude central Tasmanian sites, the Early Miocene Monpeelyata deposit (Hill and Gibson 1986a) and the Oligocene Lea River deposit (unpublished data). A single leaf from Oligocene sediments of the CIROS-1 drillhole in the Transantarctic Mountains has also been discussed (Hill 1989c, 1991a). No further specimens have been recovered from Cethana. The species is now restricted to sub-alpine habitats in Tasmania and is the only extra-South American deciduous *Nothofagus* species. The apparent thinness of the cuticle of all organically preserved fossils so far recovered indicated to these authors that the deciduous habit was present by the Oligocene at least.

Nothofagus cethanica R. Hill

Discussion. This species was also described from Cethana (Hill 1984) and considered to be very similar to two closely related New Zealand species, *N. fusca* (Hook. f.) Oerst. and *N. truncata* (Col.) Ckn. A few more specimens have been recovered and the original diagnosis is maintained.

Nothofagus aff. *alessandrii* Espinosa

Specimens examined. C-457, 665

Description. C-457 is an ovate leaf impression with excellently preserved venation, at least to the tertiary level (Fig. 14d). It is 31 mm long and 16 mm wide. The apex is acute to attenuate and the base rounded. The leaf margin has 12 regularly placed simple serrations per side and a corresponding number of secondary veins. The serrations form acute apical angles, have rounded sinuses and typically are concave on the apical side and acuminate basally. The venation is simple craspedodromous. The primary vein is rather weak and its course becomes sinuous towards the apex. The secondary veins arise at 40-45° but the lowest pair diverge at a greater angle, of about 60°. All run straight to the margin and are abruptly upcurved into the teeth. The tertiary venation is weakly percurrent (Fig. 14e) and a fimbrial vein is distinctly visible in the basal third of the leaf (Fig. 14d). Specimen C-665 is incomplete but is a larger specimen, 27 mm wide and estimated to be about 45 mm long. Its margin and available venation is the same as C-457. In addition, there is a wide stained line running midway between, and parallel to, some of the secondary veins, which is interpreted as being a result of the plicate vernation associated with deciduous leaves (Philipson and Philipson 1979).

Discussion. These fossils are indistinguishable from leaves of *Nothofagus alessandrii* (Fig. 14f) except that there are no secondary teeth or even branches from the secondary veins which lead to the margin. *Nothofagus alessandrii* is a distinctive species. Its leaves are unusual for the genus in having few (1 or 2 per secondary vein ending) secondary teeth or none in the apical half (e.g. Romero 1980; Melville 1982; Romero and Dibbern 1985; Tanai 1986; Hill and Read 1991). All of these authors

recognised that the leaves of this species appear to have more in common with some species of *Fagus*. Melville (1982) proposed an evolutionary scheme for leaf margin characters in *Nothofagus* and *Fagus* in which this condition evolved into the form of *Fagus grandifolia*, which has no secondary teeth. However, the leaf base of *Fagus grandifolia* specimens I have observed is obtuse and not broad and rounded, as in the Cethana fossils and *N. alessandrii*. Hill (personal communication) believes that in many instances fagaceous leaf impressions can not be assigned with confidence to either genus and that records of non-*Nothofagus* fagaceous leaves in the Southern Hemisphere should therefore be treated with the utmost caution. I suggest that further examination of the extent of secondary teeth in *N. alessandrii* leaves be made, as it is conceivable that populations lacking them do occur. In any event it seems illogical to refer any high latitude southern hemisphere Early Tertiary fagaceous fossils to *Fagus* since its pollen is unknown in this hemisphere, and is not recorded until the Oligocene in the northern hemisphere (Muller 1981). Contrary to previous authors, Hill and Read (1991) showed that *N. alessandrii* does have a partially formed fimbrial vein, which is a feature also shared by *Fagus*. Specimen C-457 clearly shows evidence of a fimbrial vein. Although it probably represents an extinct species with very close affinity to *N. alessandrii* the lack of secondary teeth in the Cethana fossils indicates that the possibility these fossils represent an intermediate form between *Fagus* and *Nothofagus* should not be dismissed. It is noteworthy that *N. alessandrii* has been considered to be a primitive *Nothofagus* species in that it has the highest number of seeds per cupule in the genus.

It is possible that the fossils could be assigned to one of the many South American fossil taxa considered to be similar to *N. alessandrii*, and recently revised by Romero and Dibbern (1985) and Tanai (1986), especially *N. subferruginea* (Dusen) Tanai. It is interesting that the Cethana fossils are apparently similar to the species retained by Romero and Dibbern but submerged by Tanai, *Fagus subferruginea* Dusen. This species was considered to have affinity to the North American species *Fagus grandifolia* because of a perceived lack of secondary teeth.

Nothofagus alessandrii is a deciduous species restricted to a few disjunct stands

of Chilean rainforest at about 38° S, where it occurs on shaded south facing slopes (Rodriguez *et al.* 1983). In this respect its ecology is similar to *N. gunnii*, and is very strong evidence for the maintenance of similar habitat types in these regions from at least the Oligocene. In Hill and Read's (1991) revised infrageneric classification of the genus based on cupule morphology and leaf cuticular pattern *N. alessandrii*, along with *N. gunnii* and the New Zealand species *N. fusca*, *N. truncata* and *N. solandrii* (Hook. f.) Oerst. comprise the subgenus *Fuscaspora*. Very similar morphological forms of three (or four) of these species from each of Tasmania, New Zealand and Chile therefore occur at Cethana, emphasising the point of Hill (1991a) that this subgenus was widespread across Gondwana in the Early Tertiary.

Nothofagus subgenus ***Menziesospora*** R. Hill & Read

Nothofagus tasmanica R. Hill

Discussion. This species was originally described by Hill (1983a, 1983b) from three Tasmanian Oligocene deposits, including Cethana and its diagnosis (Hill 1983a) was recently emended on the basis of abundant new specimens from these and other deposits by Hill (1991a). This diagnosis is not repeated here. Until research for the present thesis no organically preserved specimens of *N. tasmanica* from Cethana were known. Specimen C-613 has abundant organic remains, but the cuticle is poorly preserved. However, the characteristic unicellular conical trichome bases described by Hill were observed (Fig. 14g). In these and several other papers Hill has discussed the taxonomic, evolutionary and ecological implications of the marked similarity of *N. tasmanica* leaves to those of extant *N. moorei* (F. Muell.) Krasser, a species which is restricted to and dominates microthermal rainforests of the high altitude regions of northern New South Wales and southernmost Queensland. The trichome bases which are frequent along the adaxial veins of *N. moorei* and which are identical to those of *N. tasmanica* are illustrated in Fig. 14h.

cupule, aff. subgenus ***Brassospora*** Philipson & Philipson

Specimen examined. C-288

Description. The fossil is the dorso-ventral impression of a two-valved cupule with a peduncle which has become detached through fossilisation (Fig. 15a). The valves are 14 mm long and 10mm wide and the slightly curved peduncle is 8 mm long. It had a broad attachment to the cupule and narrows to the base. The valves become broader to the apical end and the apex is rounded. If the rounded portion is taken as the point at which the valves become free then they are free for about one third of their length. The impressions of four rounded lamellae are clearly visible on the valves.

Discussion. The cupule morphology of *Nothofagus* has recently been discussed in detail by Hill and Read (1991) and Hill (1991a). The Cethana specimen is quite similar in size and morphology to those from a group of extant subgenus *Brassospora* species from New Guinea with relatively massive cupule valves and to one of the two fossil species from Little Rapid River (*N. peduncularis*) described by Hill (1991a). It differs from it in having (at least) four lamellae, whereas *N. peduncularis* has only three. Of the extant species similarity is noted with species such as *N. brassii* van Steenis which has four or five lamellae (Fig. 15b).

leaf, aff. subgenus ***Brassospora*** Philipson & Philipson

Specimen examined. C-235

Description. The leaf is symmetrical and elliptic or narrow ovate, 31 mm wide and estimated to be 69 mm long (65 mm visible) (Fig. 15c). The apex is acute with a slightly retuse tip. The leaf margin has minute irregular teeth (Fig. 15d). Serration sinuses are acute with a convex basal side and usually a concave apical side. Secondary serrations are present and there are at least two serrations per secondary vein. The secondary venation is brochidodromous. The primary vein is straight and unbranched, of moderate size, with 32 ? (29 visible) alternate, thick secondary veins arising at 60-80° from the primary vein. The secondary veins are abruptly curved near the margin so that sinuous loops are formed. Loop forming branches join the superadjacent secondaries at about 90°. Tertiary vein arches are also present but

Figure 15.

(p.59)

a. Cupule, *Nothofagus* aff. subgenus *Brassospora* (C-288). The view is of the face of one valve of the cupule. There are four lamellae visible and one of them is arrowed. Scale: 5 mm.

b. Cupule of extant subgenus *Brassospora* (*Nothofagus brassii*). Scale: 10 mm.

Figs c-e. Leaf, *Nothofagus* aff. subgenus *Brassospora* (C-235). (p.59)

c. Specimen. Scale: 10 mm.

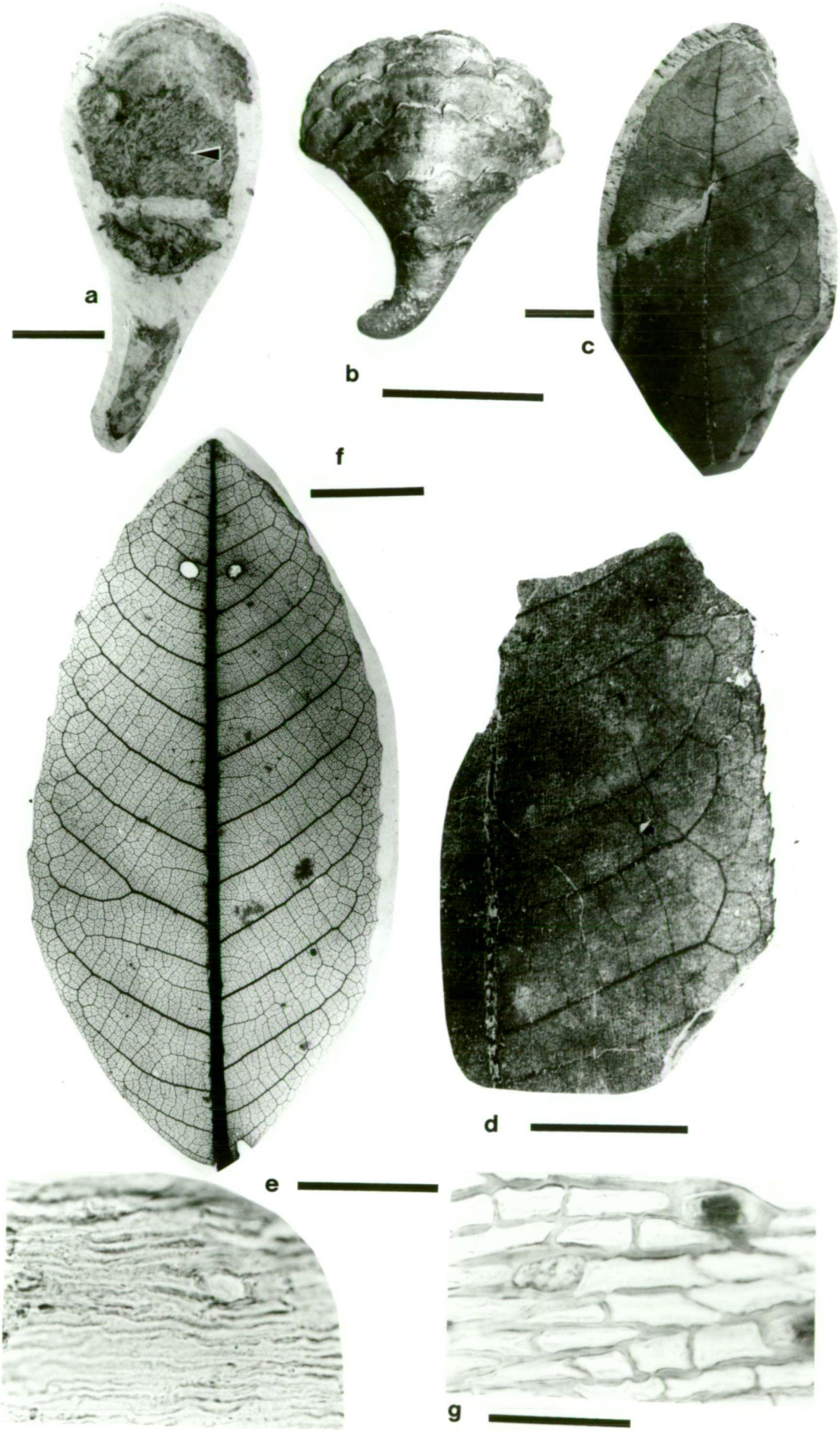
d. Enlargement of **Fig. 15c.** showing venation detail, including the fimbrial vein and serrations. Scale: 10 mm.

e. LM of trichome base from midvein cuticle. Scale: 50 µm.

Figs f, g. Extant subgenus *Brassospora*.

f. Cleared leaf of *Nothofagus pseudoresinosa*. Scale: 10 mm.

g. LM of cuticle of *N. codonandra* (Baill.) van Steenis showing trichome bases on a vein. Scale: 50 µm.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quaternary arches are poorly developed. Composite intersecondary veins occur. The tertiary veins are weakly percurrent and run oblique to the midvein. Quaternary veins are thick and a fimbrial vein is present (Fig. 15d). The leaf has glandular teeth with a vein running directly from a tertiary arch into each serration. The serration veins are eccentric to the apical side. Cutinised trichome bases occur over the midvein (Fig. 15e).

Discussion. The venation detail of specimen C-235 is extremely well preserved but cuticle is absent except for fragments from over the midvein. The leaf is markedly similar to *Nothofagus* species of New Guinea and New Caledonia. These species form a distinctive undisputed assemblage previously known as section *Calusparassus* section *bipartitae* (e.g. Hill 1983a; Tanai 1986; Dettmann *et al.* 1990) which Philipson and Philipson (1988) recently proposed should be known as subgenus *Brassospora*. Its species are all evergreen, have two-lobed cupules, no tracheids in the wood and produce a unique pollen type.

Tanai (1986) and Hill and Read (1991) recently discussed aspects of leaf form in *Nothofagus*. Most species of subgenus *Brassospora* have entire-margined leaves, but others vary from having serrations right around the margin, to those restricted to the apex where there may be only one or two small serrations present. In these species the venation is regarded as semi-craspedodromous, with the serrations being fed by minor veins arising from the secondary loops. Hill and Read (1991) note that in leaves with more strongly developed serrations (e.g. *N. discoidea* [Baum.-Bodenh.] van Steenis of New Caledonia) the veins terminating in the serrations are of a higher order. In the Cethana specimen these veins arise from tertiary loops but there are more than two serrations per secondary vein, whereas in extant species there is only one. However, there are numerous features in common with extant species such as *N. pseudoresinosa* van Steenis (Fig. 15f). These include the presence of a well developed fimbrial vein and a similar number and type of secondary veins which connect near the margin to form large loops. Unfortunately, the lack of cuticular preservation over most of the leaf makes further comparison impossible. However, trichome bases of a type which are occasionally found in subgenus *Brassospora* (Hill

and Read 1991; Hill 1991) have been observed (Fig. 15g).

Hill (1991a) described two species belonging to *Nothofagus* subgenus *Brassospora* from the Oligocene Little Rapid River deposit of Tasmania (*N. mucronata* and *N. serrata*). Both are clearly distinct from the Cethana taxon in that their serrations are only linked by a single secondary vein, but there are several other differences. Hill suggested that the presence of craspedodromous venation and the high frequency and large size of the serrations of *N. serrata* in particular compared to extant species was evidence of evolutionary process. He considered that this species had an ancestral venation type. Evolution resulted in the reduction or loss of serrations and the development of semicraspedodromous and finally brochidodromous venation. The Cethana specimen is unique in that it has numerous small but distinct teeth, but the secondary venation is clearly brochidodromous. This taxon could therefore be regarded as providing some support for this theory in that the serrations are possibly in the process of being lost. In any event it is apparent that each of the three fossil species of section *Brassospora* so far recorded from Tasmania had serrate leaves.

Currently, *Nothofagus* is dominant in the lower montane rainforests of New Guinea, New Britain and New Caledonia where cool, everwet and constantly humid conditions exist (van Steenis 1953; Ash 1982).

Discussion of *Nothofagus*. Hill (1991a) recently described new species from three of the four subgenera of *Nothofagus* (*Brassospora*, *Nothofagus* and *Menziesospora*) from the Oligocene Tasmanian Little Rapid River deposit, and reviewed the fossil record of the genus in the light of Hill and Read's (1991) infrageneric revision, and the revision of *Nothofagus* pollen types by Dettmann *et al.* (1990). At Cethana, macrofossils closely resembling extant species from Tasmania, New Guinea, northern New South Wales/southern Queensland and Chile occur. These species belong to subgenera *Brassospora*, *Menziesospora* and *Fuscaspora* of *Nothofagus*. The presence of a similar diversity of taxa in a deposit of similar age to that of Little Rapid River allows an enhanced understanding of the high latitude

vegetation of this region at this time. Various ecophysiological studies have been undertaken in an attempt to explain the co-occurrence of *Nothofagus* subgenera in the past which are now widely separated latitudinally. Thus, Read and Hope (1989) found that the tropical species have a lower frost resistance than *N. moorei*, which in turn has a lower frost resistance than *N. cunninghamii* (Hook.) Oerst. of sothern Victoria and Tasmania. In addition, Read (1990) found that the southern species have a photosynthetic tolerance of a wider range of temperatures than the New Guinean species. The likelihood that the Cethana flora is composed of elements from diverse niches provides some support for the hypothesis of Hill (1990a) that the presence of subgenus *Brassospora* in the Little Rapid River deposit is a consequence of catastrophic disturbance, and that macrofossils of this group do not usually occur in Tertiary deposits dominated by its pollen because the trees grew away from the more variable environments of regions such as lake edges. This evidence is also consistent with the gradual restriction of the *Brassospora* species to lower latitudes as the climate of southern Australia became cooler and drier with more seasonal rainfall during the Late Tertiary. The presence at Cethana (a site which would have been at about 60° S) of two *Nothofagus* species which were probably deciduous can be explained in physiological terms since there is strong evidence for a diverse topography, and by inference diverse light environments. Trees growing in heavily shaded regions such as steep south-facing slopes would have had severe stress during the long dark winters with balancing net photosynthesis and respiration. Clearly, the deciduous life form would be advantageous in such sites. In support, Read and Hill (1985) have shown that *N. gunnii* has a high light requirement for net photosynthesis with a high light compensation point and dark respiration rate. Hill (1990a) and Hill and Carpenter (unpublished data) suggest that in the Early Tertiary at high latitudes winter deciduous forests were widespread, and that as the Australian continent drifted northward most of these taxa lost their competitive edge, and became extinct.

There is also much evidence from across the range of *Nothofagus* that large-scale disturbance such as that caused by landslips in wet steeply sloped regions, earthquakes and volcanic eruptions is very important in providing large enough

canopy gaps for these typically shade intolerant taxa to regenerate (e.g. Wardle 1984; Veblen *et al.* 1981; Read and Hill 1988; Read *et al.* 1990). Extensive tectonic activity occurred during the Early Tertiary in Tasmania (e.g. Sutherland and Wellman 1986) and Hill (1991a) has suggested that subsequent geological quiescence may also have contributed to the extinction of numerous species.

Order Casuarinales

Family Casuarinaceae

aff. ***Gymnostoma*** L. Johnson

Specimens examined. C-262, 502, 777, dispersed cuticle 778, 779

Description. These specimens are represented by multi-nodal square branchlets of various lengths which have four leaves per whorl and a diameter of about 1 mm (Fig. 16a). Cuticle is well preserved on many specimens. The stomates occur in long parallel files perpendicular to the stem axis. They are confined to the shallow intercostal regions between the ridges and typically are two-to-four bands wide (Fig. 16b). The leaf sheath teeth have sparse, small but elongate papillae along their margins, are about 0.7 mm long and 0.25 mm wide and have acute apices (Fig. 16c). The nature of the sinus shape is unknown. The guard cells are overarched by one rectangular lateral subsidiary cell each and there are none, one or sometimes two epidermal cells between them. The stomatal complexes are small, with guard cells about 15-20 μm long (Fig. 16d). No trichomes or trichome bases were observed. The cuticular surface of the branchlet epidermal cells have numerous small rounded papillae.

Discussion. There have been several recent reports of *Gymnostoma* macrofossils from many Early Tertiary sites in Australia (e.g. Christophel 1980; Dilcher *et al.* 1990; Scriven and Christophel 1990) and there is no doubt that these plants grew in high rainfall environments at least along watercourses. These authors, Johnson and Wilson (1989) and Wilson and Johnson (1989) have discussed the characters which can be used to distinguish *Gymnostoma* from the other Casuarinaceae (*Ceuthostoma*, *Allocasuarina* and *Casuarina*). The Cethana specimens have clear

Figure 16.

Figs a-d. aff. *Gymnostoma*. (p. 63)

a. C-778. SEM of stem section at a node. Three of the four scale leaves are visible, but no stomates. Scale: 100 μm.

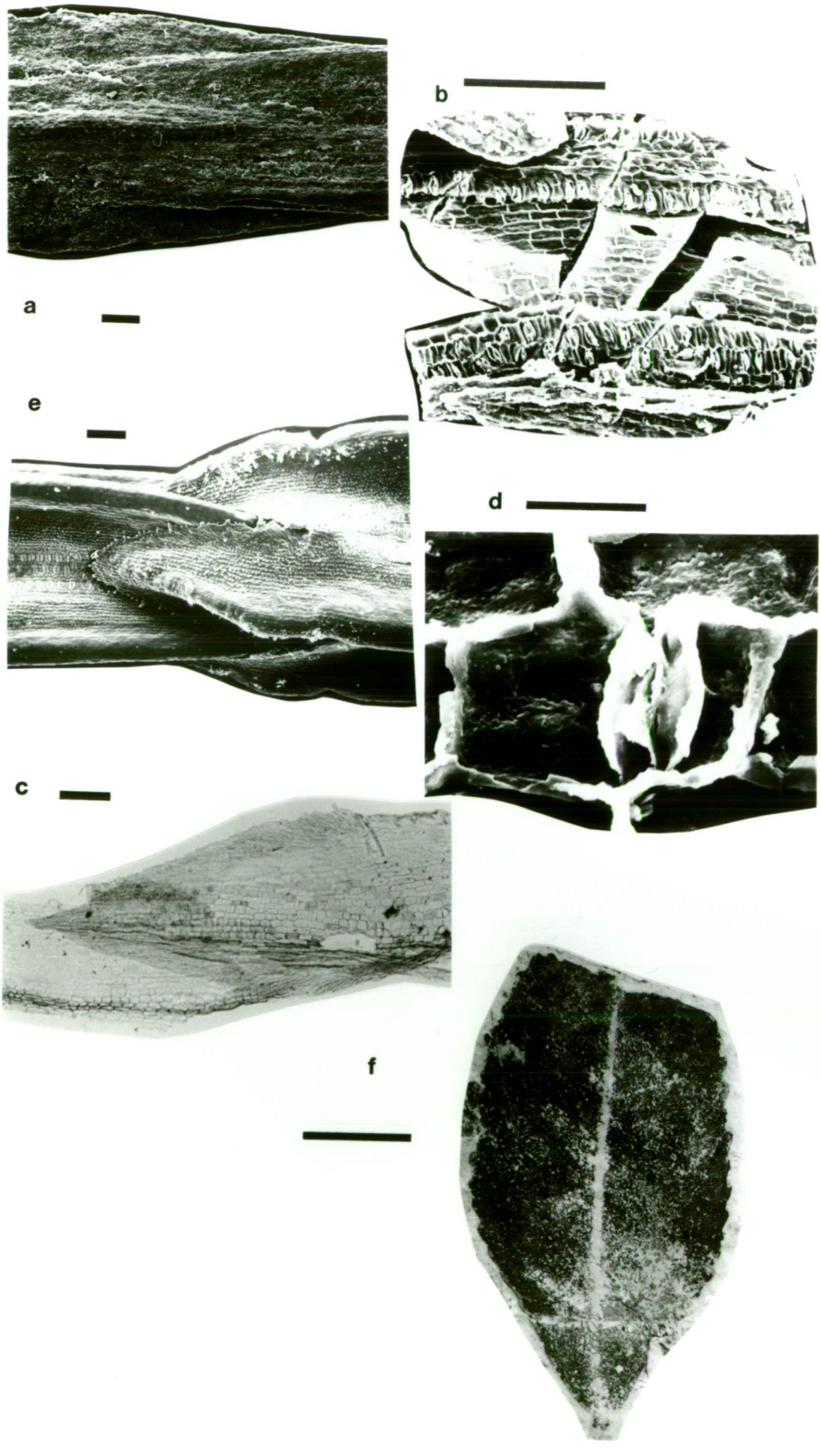
b. C-779. SEM of inner cuticle surface showing rows of stomates. Scale: 100 μm.

c. C-502. LM of stem section at a node showing a leaf sheath tooth with some small papillae at top right. Scale: 100 μm.

d. C-779. SEM of stomate. The lateral subsidiary cells overarch the guard cells. Scale: 10 μm.

e. SEM of stem section of extant *Gymnostoma australianum* Johnson, showing the location of stomates in furrows between segments. Scale: 100 μm.

f. aff. Elaeocarpaceae (C-608) leaf. Scale: 10 mm. (p. 64)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affinity to *Gymnostoma* in that the stomates occur in glabrous, apparently shallow furrows between the branchlets. In the other genera the furrows are deep and narrow and trichomes are usually present within them. The stomates are concealed within these furrows. All fossil branchlets so far examined are roughly square in cross-section and four-parted with whorls of four teeth at the summit of each article. This also conforms entirely to *Gymnostoma*. However, four parted branchlets also occur in *Ceuthostoma* and a few species of *Allocasuarina*, so this character is not diagnostic. Further research on Cethana specimens, including a possible mature female infructescence, is required before an unequivocal determination of *Gymnostoma* can be made, and to be certain that no other casuarinaceous taxa occur. In particular, it is difficult to discern whether there are deep furrows present when stems are compressed. Extant *Gymnostoma* species occur in Malesia (especially New Guinea), New Caledonia, Fiji and one species in north-eastern Queensland (Fig 16e), and are usually found on open sites with oligotrophic soils. Macrofossils occur in numerous other Oligocene Tasmanian deposits (Hill 1990a).

Order Malvales

Elaeocarpaceae

aff. ***Elaeocarpus*** L.

Specimen examined. C-608

Description. This ovate leaf is incomplete at the apex but is confidently estimated to be 55 mm long and is 26 mm wide (Fig. 16f). The leaf base is acute. The margin is regularly serrate with glandular tipped teeth placed at approximately 2 mm intervals. The sinus angle is acute and the basal side of the teeth is prominently convex. The venation is semicraspedodromous. There are probably 15-20 weakly defined secondary veins which arise at variable but usually high angles from the midvein. These form loops about 3 mm in from the margin. Cuticle is fragmentary except along the midvein. The leaf is hypostomatic. Very thick, heavily stained trichome bases occur abundantly along the midvein (Fig. 17a). Larger glands also occur at least on the adaxial leaf surface (Fig. 17b). The stomates are randomly

Figure 17.

(p. 64)

Figs a-c. aff. Elaeocarpaceae (C-608). LM's of cuticle.

a. Thickened trichome bases along a vein. Scale: 100 μm.

b. Large glandular trichome base. Scale: 10 μm.

c. Stomate. Scale: 10 μm.

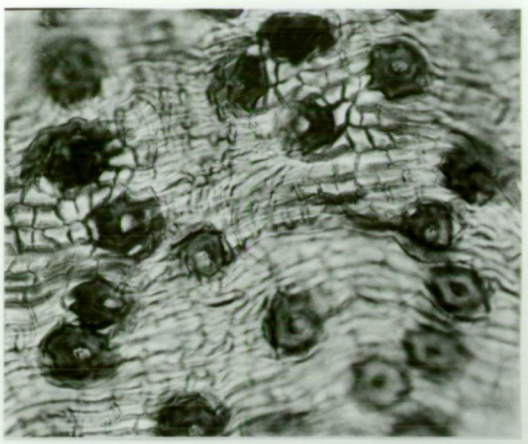
Figs d-f. Extant *Elaeocarpus* species. LM's of cuticle.

d. *E. holopetalus*. Trichome bases from a vein on the adaxial side. Scale: 100 μm.

e. *E. reticulatus*. Large glandular trichome base. Scale: 10 μm.

f. *E. reticulatus*. Stomate. Scale: 10 μm.

a



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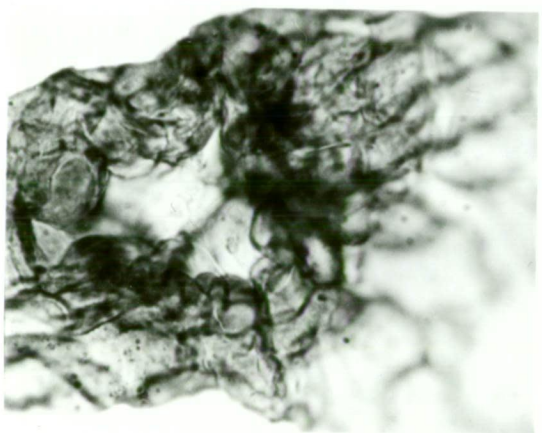

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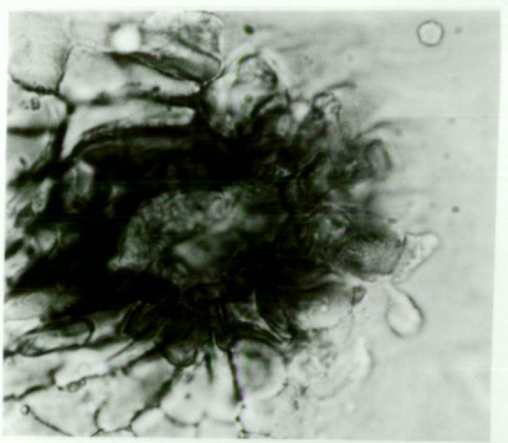

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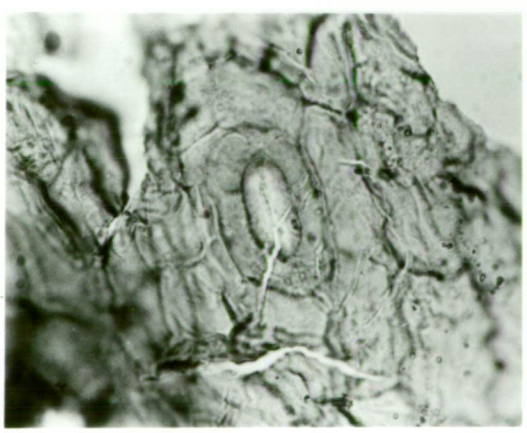

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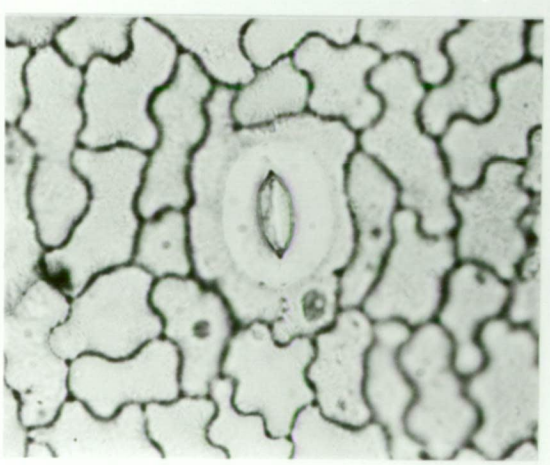

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distributed and have an oval shape in outline around the stomatal pore (Fig. 17c). The epidermal cell anticlinal walls are slightly sinuous.

Discussion. Although investigation of this specimen is preliminary and only three extant species of *Elaeocarpus* have been used for comparison there are at least three highly distinctive cuticular characters in addition to the leaf architecture which conform entirely to this genus. These are the presence of identical trichome bases (Fig. 17d), glands (Fig. 17e) and similar stomates (Fig. 17f). *Sloanea* has been considered to be very similar to *Elaeocarpus* (Christophel and Greenwood 1987) and there is no doubt that aspects of the cuticular morphology of *S. australis* (Benth.) F. Muell. are similar. However, at least in terms of leaf morphology the fossil is quite distinct from the Australian species of *Sloanea* examined. In particular, the leaf blade of *S. australis* is narrowed towards the base and then winged before its junction with the petiole, and this and the other species do not exhibit anywhere near the frequency of serrations as the fossil. Therefore, although there are numerous extra-Australian species of *Sloanea* (and *Elaeocarpus*) which were not studied it is probable that the affinity of the fossil lies with *Elaeocarpus*. *Elaeocarpus* is a rainforest genus of about 200 species which occurs in eastern Australia, Madagascar, Asia, Malesia (especially New Guinea), western Pacific Islands and New Zealand (Floyd 1989). *Elaeocarpus* like leaves have been reported from several Early Tertiary deposits in south-eastern Australia (e.g. Christophel and Greenwood 1987; Christophel *et al.* 1987), but none have been described. Rozefelds (1990), however, has described several fossil *Elaeocarpus* endocarps and discussed the quite extensive record of the genus in Australia.

Sterculiaceae

aff. ***Brachychiton*** Schott et Endl.

Specimen examined. C-648

Description. The fossil is represented by an incomplete but large lobed leaf on which one lobe is mostly complete (Fig. 18a). From the leaf base this is 135 mm long (estimated to be 145 mm long when complete) and is 28 mm wide. It is free along its apical margin for at least 100 mm but the presence of three primary veins at

Figure 18.

Figs a-c, e, f. aff. *Brachychiton* (C-648). (p. 65)

a. Leaf. The right lobe is mostly complete and the three primary veins arising from the leaf base are visible (arrowed). Scale : 10 mm.

b. SEM of inner abaxial cuticle surface showing cutin coverings over the stomates, and depressions which correspond to the papillae seen on the surface. Scale: 100 µm.

c. LM of abaxial cuticle showing a water stomate (arrowed), stomatal regions (especially at bottom) and papillae on the veins. Scale: 100 µm.

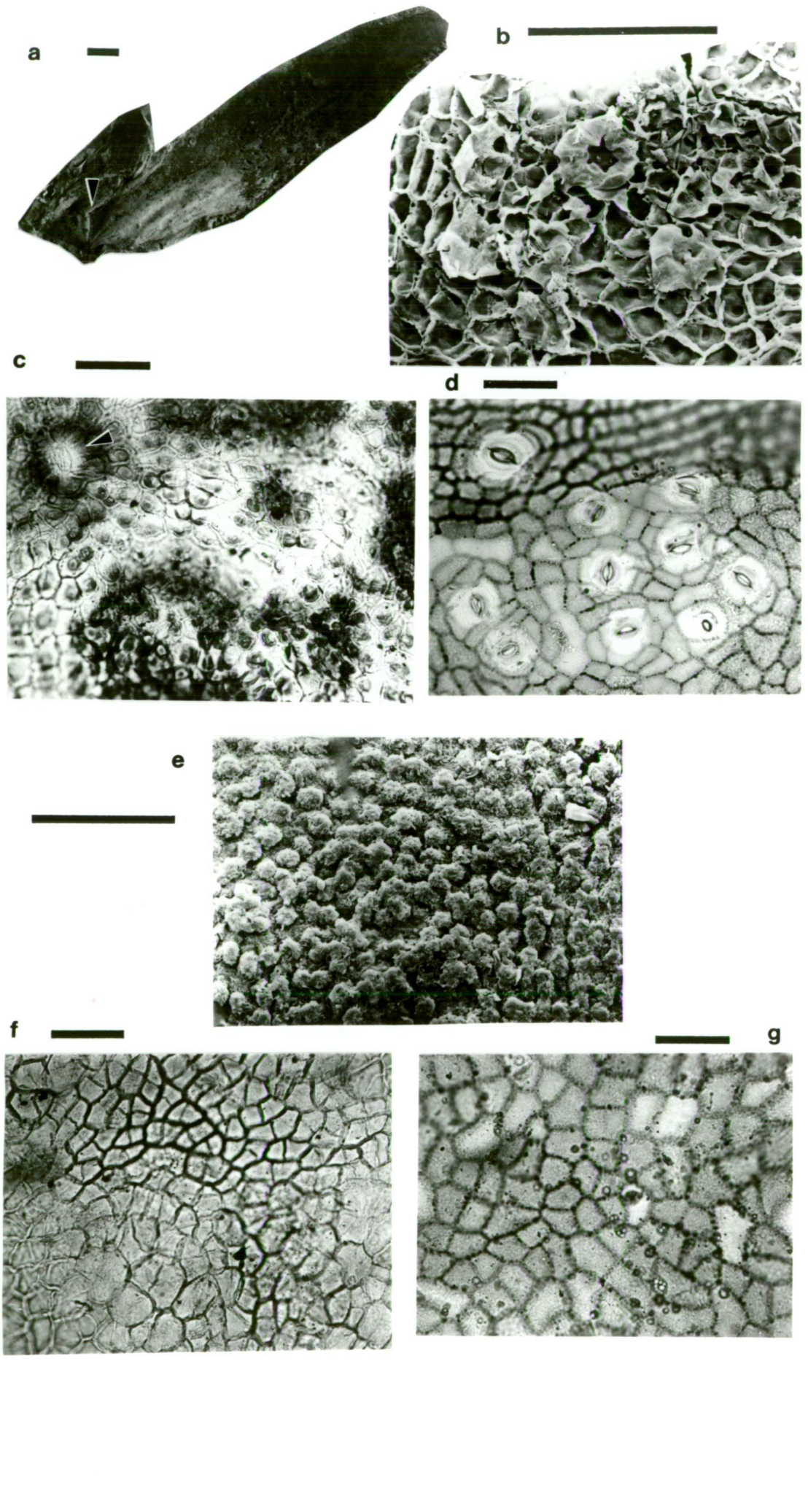
e. SEM of outer abaxial cuticle surface showing papillae. Scale: 100 µm.

f. LM of adaxial cuticle. Scale: 100 µm.

Figs d, g. Extant *Brachychiton acerifolium.*

d. LM of abaxial cuticle showing a water stomate on a vein and a stomatal region. Scale: 100 µm.

g. LM of adaxial cuticle. Scale: 100 µm.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the base indicates that the leaf had three primary lobes. The venation is actinodromous with the primary veins arising basally and of the perfect, marginal type. The venation in the apical region of the lobe is brochidodromous. The leaf margin is entire and apparently thickened. The cuticle is thick and the stomates are restricted to the abaxial surface where they are found in the regions between the minor veins. Individual stomates are impossible to observe in detail because of the presence of a covering of cutin masking the stomatal apparatus (Figs 18b, c). Water stomates are present over veins (Fig. 18c) and each abaxial epidermal cell has a prominent surface papilla (Fig. 18c, e). The adaxial cuticle is featureless and composed of straight walled epidermal cells (Fig. 18f).

Discussion. There is considerable evidence that this leaf can be referred to *Brachychiton*. In particular, the actinodromous, palmately lobed entire margined leaf morphology is highly distinctive. However, of the 31 species recognised by Guymer (1988), the cuticles of only three have been examined, and although there are similarities, the cuticle of the fossil specimen has several unique features which require further examination and comparison to other extant species, before the fossil can be assigned to *Brachychiton* with confidence. The distribution of the stomates and the nature of the water stomates and adaxial cuticle are very similar to those of extant species such as *B. acerifolium* (A. Cunn. ex G. Don) F. Muell. (Figs 18d, g). However, the remarkable masking of the stomates and the distinctive thickened papillae were not observed in the extant species. These features suggest that the fossil species was evergreen and they may have been an adaptation for limiting water loss from the stomates. Although some species of *Brachychiton* are found in the rainforests of eastern Australia most occur in semi-arid monsoonal regions of northern Australia. Most species are obligately deciduous or semi-deciduous during the dry season but remarkably *B. gregorii* (F. Muell.) Diels which is restricted to arid Central Australia, is evergreen (Guymer 1988). Specimens of *B. gregorii* have yet to be examined but it is interesting that, according to Guymer's descriptions and illustrations, the leaf form of the fossil is most similar to that of this species. The genus is found in all states of Australia (except Tasmania) and in New Guinea. Three

lobed *Brachychiton* fossils are known from Eocene deposits at Golden Grove (Christophel and Greenwood 1987) and Anglesea (Christophel *et al.* 1987).

Order Rosales

Family Cunoniaceae

Callicoma Andr.

Callicoma serratifolia Andr.

Specimens examined. C-480 (leaf), C-531 (infructescence)

Callicoma is a monospecific genus. *C. serratifolia* is endemic to coastal eastern Australia from the Batemans Bay district of southern New South Wales to near Gladstone, coastal central Queensland (Floyd 1989). It is an abundant species usually associated with rainforest margins and scrub along watercourses and occurs from sea level to the ranges. Dickison (1975) recorded the leaf venation type of *C. serratifolia* as simple craspedodromous and noted the presence of two trichome types. In a more detailed study Kennedy and Prakash (1981) disputed some of Dickison's findings. They detected two distinct groups within the species which they designated groups A and B. Major morphological differences between groups A and B included the serration type, distribution of trichomes on stems and branches, overall leaf size and venation pattern. No intermediates were found even though the authors noted that the two forms exist side by side in the same localities. According to Kennedy and Prakash leaves from group A (Fig. 19a) have craspedodromous venation, mostly saw-toothed margins, are up to 120 x 60 mm and have a single trichome type (paired thin hairs with a small diameter base) whereas those of group B have cladodromous venation, mostly double saw-toothed margins, are up to 180 x 90 mm and in addition to having the group A type, have straight thick trichomes. The specimens they studied were from the Dorrigo and Grafton regions. Examination of six herbarium specimens of *C. serratifolia* and their cuticles confirms that there is morphological variation within the species although other findings by Kennedy and Prakash are dubious or need clarification. In particular, it is doubtful that any leaves of *Callicoma* have cladodromous venation. Also, *C. serratifolia* has no "thick" trichomes. Rather, these

Figure 19. Cunoniaceae. ***Callicoma serratifolia***

Figs a, b, g, h. Extant Group A leaf morphotype.

a. Leaf. Scale: 10 mm.

b. LM of a large trichome base and trichome from a secondary vein on the abaxial side. Scale: 10 µm.

g. SEM of inner abaxial cuticle surface showing paired small trichome bases (at top and bottom centre left) and stomates. Scale: 10 µm.

h. SEM of inner adaxial cuticle surface. A trichome base is at bottom left. Scale: 50 µm.

Figs c-f, i. C-480. (p. 67)

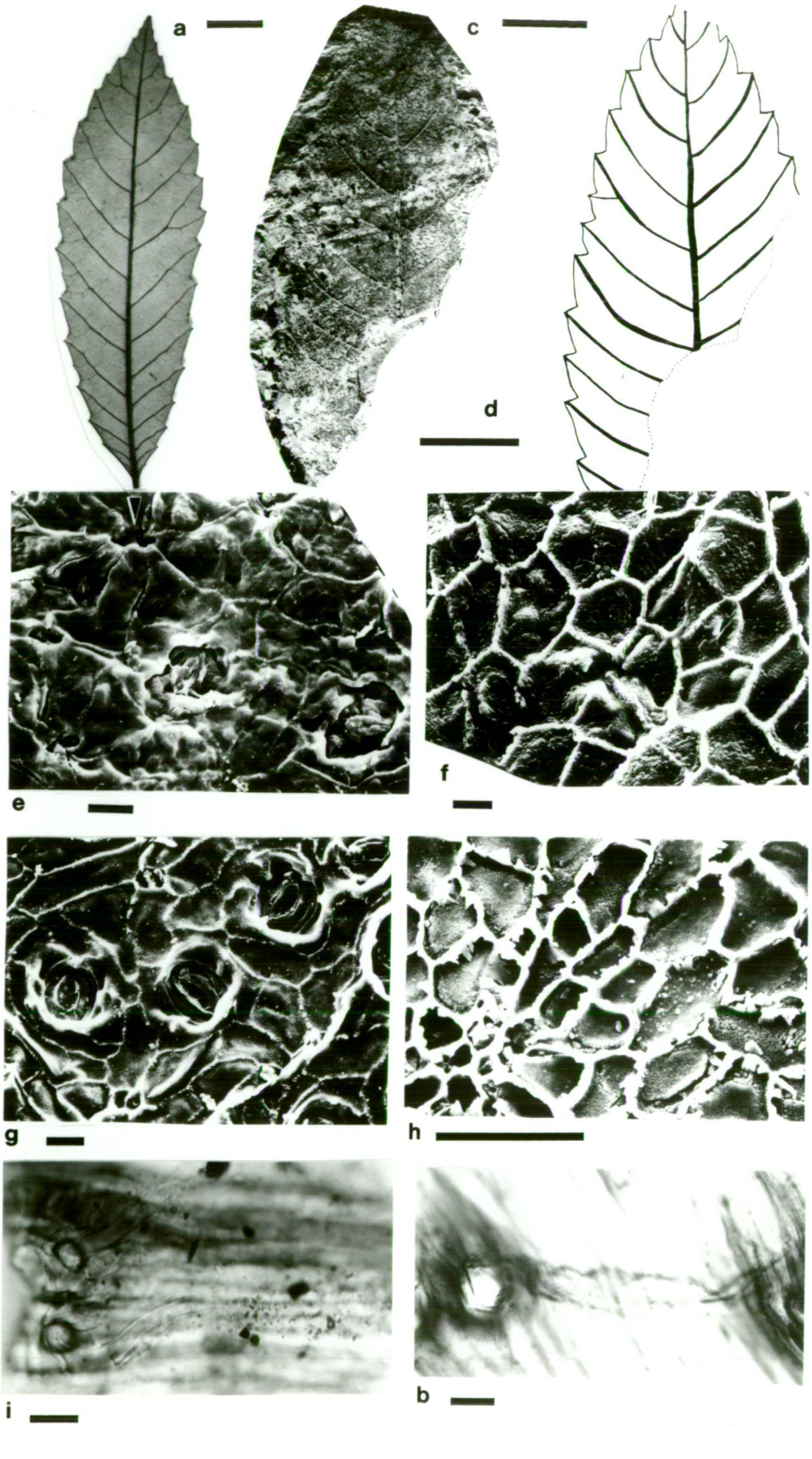
c. Leaf. Scale: 10 mm.

d. Drawing of **Fig. 19c** to show venation. Scale: 10 mm.

e. SEM of inner abaxial cuticle surface, showing paired small trichome bases (arrowed at top left) and stomates. Scale: 10 µm.

f. SEM of inner adaxial cuticle surface. Scale: 10 µm.

i. LM of venous cuticle showing two large trichome bases with preserved trichomes. Scale: 10 µm.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are thinly cutinised trichomes with a much greater diameter and the basal cells are variously thickened, a feature discernable using LM because of the often heavy staining in these regions (Fig. 19b). They do occur in Group A, but only on the adaxial surface and along major veins on the abaxial surface. They are not found distributed amongst the stomata on minor veins as in Group B, and presumably this is what Kennedy and Prakash meant when they referred to Group A leaves having only one trichome type. Only one of the six specimens examined could clearly be assigned to Group B, and this was the only specimen from the Dorrigo region.

The fossil leaf, although incomplete at the base and apex, conforms to Group A. It exhibits mostly simple saw-toothed serrations, craspedodromous venation, and is estimated to be about 65 mm x 25 mm (Fig. 19c, d). There are probably about 15 serrations per side and a similar number of secondary veins. The inner surfaces of the adaxial and abaxial cuticles of fossil (Figs e, f) and extant (Figs g, h) specimens are indistinguishable. Two types of trichome (or their bases) are present on the fossil cuticle. The first is visible as a small round aperture with a relatively unthickened rim (Fig. 19e). This type is usually paired and apparently restricted to the stomatiferous regions of the abaxial surface, being absent from the major veins. The other type is found on the adaxial surface and only along major veins on the abaxial surface. The base of these trichomes has a much greater diameter and the cells surrounding it are often heavily thickened. Some trichomes of this form are preserved intact and are thinly cutinised tapering extensions about 75 µm long (Fig. 19i). Another feature of *Callicoma* cuticle is the frill-like margin around the stomatal apparatus (Figs 19e, g).

Since the fossil leaf is identical to one of the morphotypes (Group A) of *C. serratifolia* recognised by Kennedy and Prakash (1981) it should be assigned to that species.

According to Engler (1930) *Callicoma*, along with the New Caledonian endemics *Codia* and *Pancheria* comprise the tribe Pancherieae. Leaves of *Pancheria* and *Codia* were studied. Cuticles of two of the four species of *Codia* examined (*C. albifrons* Viell. ex Guillaum. and *C. discolor* [Brongn. & Gris.] ex Guillaum.) share many remarkable similarities with that of *Callicoma*. These are the presence of both

trichome types, including the paired form, and the remarkable similarity of the frill around the stomatal pit (Fig. 20a). These features have not been observed in any of the other cunoniaceous genera, and indicate, along with the fact that the inflorescences of these genera are very similar, that they have a close phylogenetic relationship. *Codia* leaves are easily distinguishable from those of *C. serratifolia* since they are entire margined whereas those of *C. serratifolia* are distinctively saw-toothed.

Flowers of the tribe Pancherieae are formed in tightly packed globose clusters (Engler 1930; Dickison 1984). Those of *C. serratifolia* have a diameter of 10-20 mm but reduce to 8-10 mm with the loss of the stamens and styles following fertilisation (Fig. 20b) (Floyd 1989). The flowers are bisexual, apetalous and bicarpellate (Kennedy and Prakash 1981). The fossil compression has a diameter of about 8 mm (Fig. 20c). The loss of the three-dimensional form makes detailed interpretation of the specimen difficult but the valves of numerous open capsules are clearly visible around the perimeter of the infructescence. Material of *Codia* and *Pancheria* was not examined. However, organic fragments of the fossil infructescenses were found to include heavily striated tuberculate cuticular remains (Fig. 20d). This cuticle is identical to that found on the seed coats of *C. serratifolia*, as described and illustrated by Dickison (1984) and Kennedy and Prakash (1981) and illustrated in Fig. 20e. Seeds of *Codia* and *Pancheria* are smooth (Dickison 1984), so the fossil infructescence can be assigned to *Callicoma* with confidence. No other organic matter yielded cuticular remains. There is no organic connection between leaves and infructescences, but no reason for regarding them as being derived from different taxa. Therefore both leaves and fruits of *C. serratifolia* occur in the Cethana sediments.

Vesselowskya Pampan.

Vesselowskya aff. ***rubifolia*** (F. Muell.) Pampan.

Specimens examined. C-620, 621

Description. Specimen C-620 is a compound (trifoliate ?) leaf in which the impression of only one leaflet is preserved. C-621 is an isolated leaflet with some

Figure 20. Cunoniaceae

a. SEM of inner abaxial cuticle surface of extant *Codia discolor*. Note the similarity to *Callicoma* (**Fig. 19e, g**) including the presence of paired small trichome bases (arrowed at top left). Scale: 50 μm.

Figs b-e. *Callicoma serratifolia* infructescences. (p. 69)

b. Mature extant specimen. Note the opened capsules. This specimen has remnant stamens which may later become detached. Scale: 5 mm.

c. C-531. Opened capsules are visible around the perimeter of the specimen. The stamens have apparently been detached. Scale: 5 mm.

d. SEM showing the outer surface of cuticle obtained from C-531. Scale: 100 μm.

e. SEM showing the surface of an extant seed. Scale: 100 μm.

Figs f, h, i, k. *Vesselowskya* aff. *rubifolia* (C-621). (p. 69)

f. Apical portion of leaflet. Note the small serrations. Scale: 10 mm.

h. Enlargement of the counterpart of that portion of the specimen illustrated in **Fig. 20f** to highlight the venation. The impression of the dense vestiture is visible along the major veins (arrowed). Scale: 5 mm.

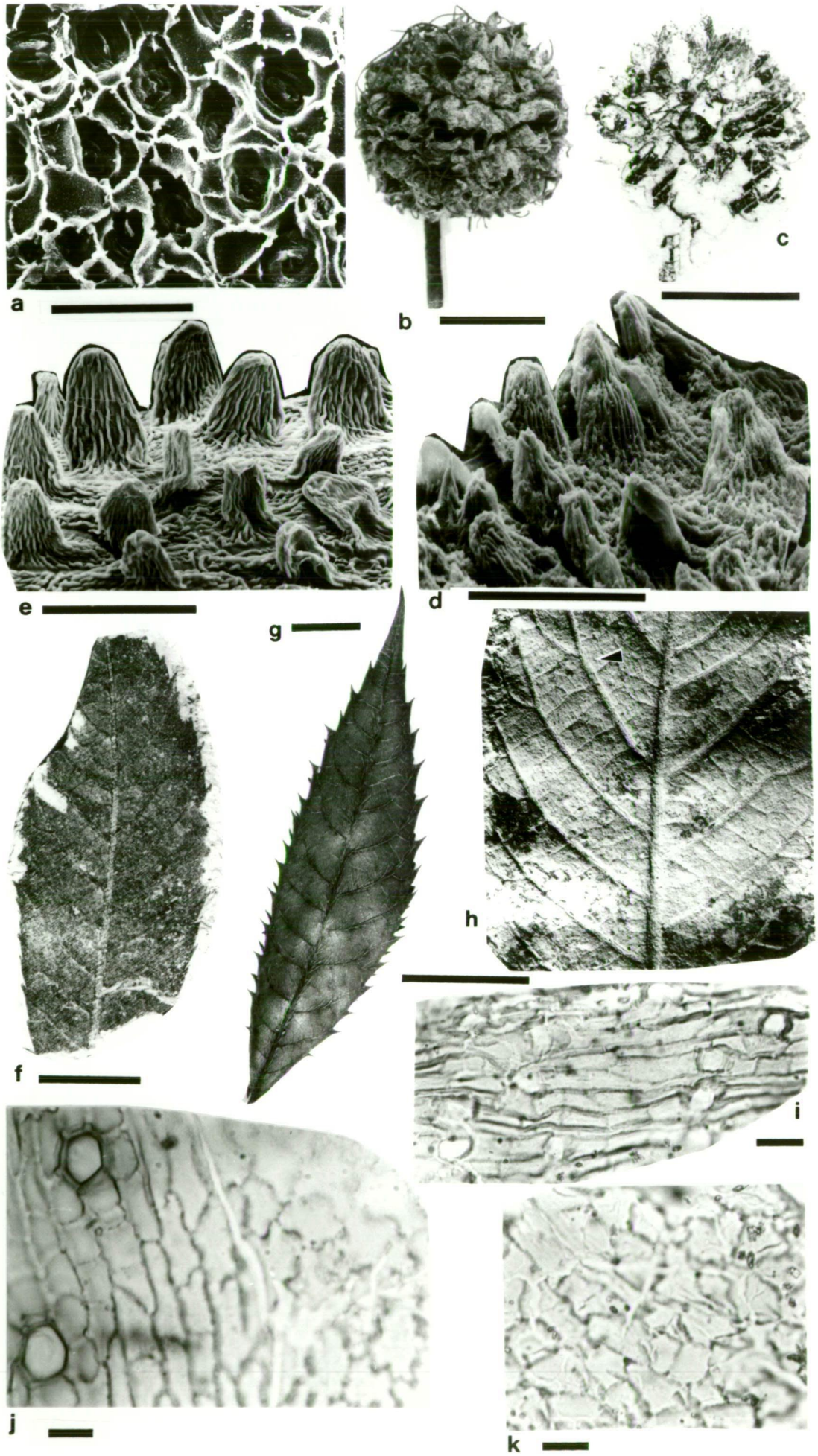
i. LM of cuticle showing trichome bases. Scale: 10 μm.

k. LM of adaxial cuticle showing small epidermal cells with vaguely sinuous walls. Scale: 10 μm.

Figs g, j. Extant *Vesselowskya rubifolia*.

g. Leaflet. Note the serrations, venation and vestiture. Scale: 10 mm.

j. LM of adaxial cuticle showing trichome bases and epidermal cells. Scale: 10 μm.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cuticular preservation (Fig 20f). The leaflets are up to about 60 mm long with simple craspedodromous venation. The secondary veins are frequently once-forked and end in pungent serrations and the leaflet apex ends in a spinose tip.

Discussion. *Vesselowskya* is a monospecific genus and *V. rubifolia* is found from the Hunter River to the Clarence River in New South Wales and in New Caledonia, although the latter population may be a distinct species (Floyd 1989). The venation and surface details of the fossil leaves are excellently preserved, and are very similar to those of the extant species (Fig. 20g). A distinctive feature of *V. rubifolia* leaves is a dense vestiture, particularly along the midvein and lateral veins of the abaxial surface. Low angle illumination clearly displays this feature on specimen C-621 (Fig. 20h), as well as the simple craspedodromous venation, where all but a few apical and basal secondary veins are branched at about two thirds of their length and end in serrations. The two specimens each have about 16 secondary veins and 25 serrations. One of the secondary veins of specimen C-621 is secondarily branched. The percurrent forked tertiary veins oblique to the midvein are also visible. The leaf apex ends in a fine point similar to those of the serrations. All of these venation features have been observed in *V. rubifolia.* The extant species has compound leaves with three to five leaflets radiating from the petiole. Specimen C-620 is interpreted as being a leaflet of a compound leaf which was displaced downwards by an angle of at least 90 degrees during fossilisation. Its long petiolule suggests that it was the central leaflet. The petiole is similar in length to that of *V. rubifolia.* Organic matter is preserved along the midrib of specimen C-621 and cuticle fragments were recovered. Like that of *V. rubifolia*, the cuticle is quite thin. Similarly, the trichomes and trichome bases (Fig. 20i) of the fossil are indistinguishable from those of *V. rubifolia* (Fig. 20j) as are the few stomata present and the epidermal cells on the adaxial surface (Fig. 20k). These cells are unlike those of all other Cunoniaceae examined in being small with vaguely sinuous walls.

The specimens may represent a distinct species since the serrations of the fossil leaves are not as pronounced (Fig. 20a) as in all specimens of *V. rubifolia* examined. However, there seems little doubt of a very close relationship.

Weinmanniaphyllum R. J. Carpenter gen. nov.

Diagnosis. Leaves imparipinnate with multiple sessile lateral leaflets. Terminal leaflet elongated. Leaflets serrate margined, venation semi-craspedodromous. Petiole between leaflet pairs winged.

Type species. *Weinmanniaphyllum bernardii.*

Discussion. A new genus is proposed here to encompass foliage that is indistinguishable from that of some species of *Cunonia* and *Weinmannia*, but which lacks cuticular preservation.

Weinmanniaphyllum bernardii sp. nov. (Figs 21a-e)

Diagnosis. Leaves with up to at least 12 pairs of lateral leaflets. Lateral leaflets symmetrical, elliptic, with acute apex and base and regular serrations with acute apical angles. Serrations usually straight on the apical side and convex basally with an angular sinus. Number of serrations usually 15. Winged petiole region ovoid and entire margined, sometimes asymmetrical. Primary vein of moderate size and straight. About 18, usually alternate secondary veins arise at 60-80° from the primary vein, the lowest pair more acute than the pairs above it. Principal serration vein eccentric toward the apical margin and deflected. Tertiary veins reticulate. The terminal leaflet is elongated by a factor of about 1.5 and has about twice the number of serrations and veins as the lateral leaflets.

Specimens examined. C-033, 060, 138, 356, 377, 638, 639, 645, 663, 664

Holotype. C-377; Department of Plant Science, University of Tasmania.

Type locality. Cethana, Tasmania.

Etymology. The specific epithet refers to L. Bernardi, who revised the taxonomy of *Weinmannia*, and recognised the biogeographic significance of the genus.

Discussion. According to Bernardi (1961, 1963a, 1963b, 1964) there are over 130 species of *Weinmannia* widely distributed across the southern hemisphere, with a few extending north in Central America and Malesia. By far the greatest

Figure 21. Cunoniaceae

(p. 71)

Figs a-e. *Weinmanniaphyllum bernardii.* Portions of leaves.

a. C-060. Scale: 10 mm.

b. C-377. Note the elongated terminal leaflet. Scale: 10 mm.

c. C-356. Scale: 5 mm.

d. Enlargement of part of C-060 to highlight the semi-craspedodromous venation of the leaflets and the winged interpetiolar regions. Scale: 5 mm.

e. Drawing to show venation of C-060. Scale: 5 mm.

f. Extant*Weinmannia tannaensis*. Scale: 10 mm.


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number of species are known from Andean South America where it seems likely that much speciation has occurred, related to the uplift of these mountains. The closely related genus *Cunonia* has about twenty species in New Caledonia and a single outlier in South Africa. Herbarium specimens of over 40 species of *Weinmannia* and 10 of *Cunonia* were examined. The genera are segregable on slight differences in floral and seed morphology (Engler 1930; Bernardi 1964; Dickison 1984) where the seeds of *Weinmannia* are always hirsute and those of *Cunonia* winged. Vegetatively, including evidence from preliminary cuticle studies, species of these genera are very difficult if not impossible to distinguish. It is therefore not surprising that Cronquist (1981) considers that the two genera may best be combined.

Fossils of *Weinmanniaphyllum* are quite common in the finely laminated siltstones with alternating sand layers described by Hill (1984), however none have been collected with preserved cuticle. Despite this these fossil leaves can be assigned to *Weinmannia* or *Cunonia* with confidence since they share a unique combination of distinctive vegetative characteristics with some species of these genera. These features are;

1) Compound imparipinnate leaves and multiple pairs of sessile lateral leaflets with semi-craspedodromous venation (Figs 21a-e)

2) The presence of winged or flanged regions between successive pairs of leaflets (Figs 21a-e)

3) Leaves with an elongated terminal leaflet (Fig. 21b).

A winged petiole has also been observed in the Davidsoniaceae, Sapindaceae (*Harpullia alata* F. Muell.) and Proteaceae (*Hicksbeachia pinnatifolia* F. Muell., *Turrillia bleasdalei* [F. Muell.] A. C. Smith), but there are numerous morphological differences between these taxa and *Weinmannia* and *Cunonia*, not least including leaf size and the type and arrangement of serrations. The characters outlined above are significant for the current infrageneric taxonomy of these genera. According to Bernardi (1961) there are numerous American species of *Weinmannia* section *Weinmannia* with this leaf form, especially in series *Pinnatae*. However, the winged petiole is unusual and is rarely as fully developed outside the American region,

although it is not limited to section *Weinmannia*. In the Australia- New Guinea region only one (little known) species exhibits this character. This is *W. versteeghii*, described by Perry (1949) from the Lake Habbema district of montane New Guinea. However, a few of the Pacific and Indian Ocean imparipinnate species possess this character, including *W. tinctoria* Sm. of the Mascarenes, *W. serrata* Brongn. et Gris. of New Caledonia and *W. denhamii* Seem. and *W. tannaensis* Guillaum. (Fig. 21f) of Vanuatu (Bernardi 1963a). In addition, *Cunonia* has several species endemic to New Caledonia which also have imparipinnate leaves with a winged petiole, especially *C. pterophylla* Schltr. The fossil leaves were quite thick, and the venation distinctly raised on one surface (presumably the abaxial side). There were up to twelve pairs of lateral leaflets, which is beyond the range of any living *Cunonia* species (Engler 1930) and may suggest a closer affinity with *Weinmannia*. The lateral leaflets are typically about 17 mm long and 7.5 mm wide and the winged region about 9 mm long and 3 mm wide. However, two specimens are much smaller (C-138, 356 [Fig. 21c]). Since these are morphologically identical to other specimens they are presumed to represent foliage from new growth.

Discussion of Cunoniaceae. The Cunoniaceae is a rather diverse assemblage, being comprised of genera with a range of foliar morphologies (Dickison 1975) and fruit types, including dehiscent follicles and indehiscent dry capsules and fleshy drupes and berries (Dickison 1984). Representatives now occur in each major landmass and numerous islands of the Southern Hemisphere. The centre of diversity is in eastern Australia. *Caldcluvia* was enlarged by Hoogland (1979) and is one of the few woody genera (others include *Nothofagus* and *Podocarpus*) common to Australia, New Guinea, New Zealand and Chile. It therefore exemplifies the Gondwanic history of the family. The distribution of *Cunonia* is remarkable, being found in South Africa and New Caledonia. *Weinmannia* is by far the largest and most widespread genus (over 130 species), being found in South and Central America, New Zealand, Pacific Islands, Malesia and Madagascar. Its presence in these regions but not Australia and South Africa is somewhat enigmatic.

There was clearly a striking diversity of cunoniaceous plants growing around the site of deposition at Cethana in the Early Oligocene. In fact, several other taxonomically distinct specimens with affinity to members of the family are under investigation. These include impressions of mature *Schizomeria* and *Acsmithia* flowers and a compression of a *Ceratopetalum* leaf(-let) with well preserved cuticle. This tally so far identified may be regarded as a fraction of the total taxa in the region since taphonomic factors restrict or heavily bias potential fossils toward organs from plants growing immediately adjacent to depositional sites.

An examination of the literature reveals few detailed ecological studies concerning the family. However, species of four of the genera referred to here (*Callicoma*, *Vesselowskya*, *Schizomeria* and *Ceratopetalum*) may now be found together in the rainforests of north-eastern New South Wales, particularly in regions where the warm and cool temperate rainforest associations described by Baur (1957) intergrade on the poorer soil types. *C. serratifolia* is restricted to New South Wales and southern Queensland and *V. rubifolia* is confined to upland scarp regions of the New South Wales Great Divide, usually in association with *Nothofagus moorei* in microthermal rainforest. *N. tasmanica*, one of the dominant taxa in the Cethana flora, has been shown by Hill (1983b) to be virtually identical to this species. Therefore, a distinct element of the Cethana flora can be regarded as having strong relationships with the *N. moorei* forests of regions such as the Dorrigo escarpment and Mt Banda Banda. These data therefore fulfill the prediction of Hill *et al.* (1988) that *C. apetalum* D. Don and *V. rubifolia*, or their immediate ancestors, once occurred in Tasmania but were unable to adapt or evolve to the changing conditions in Tasmania from the middle Tertiary onwards. These authors could have included *C. serratifolia* with this group as, although it occurs in other vegetation types, it is frequently associated with *N. moorei*. This general region of northern New South Wales and southern Queensland (the Macpherson-Macleay Overlap) has long been known for its important rainforest massifs (Burbidge 1960), and it includes environments suitable for each of microthermal, mesothermal and megathermal vegetation in close proximity (Nix 1982).

However, the temperate rainforest of north-eastern New South Wales is not the only example of extant vegetation where species with close affinity to Cethana taxa occur, since *Ceratopetalum*, *Schizomeria*, and *Weinmannia* are all elements typical of lower-upper montane rainforest in New Guinea (Johns 1982; Paijmans 1976). Members of the family are also common in New Caledonia, Fiji and northeastern Qld.

Confirmed Tertiary macrofossil records of the Cunoniaceae in Australia are scant although there is no doubt that macrofossils assignable to the family occur in many deposits, including the Oligo-Miocene Yallourn and Morwell coals (Blackburn 1985). Ettingshausen (1888) described a species of *Callicoma* from Vegetable Creek, New South Wales (Tertiary) and four species of *Ceratopetalum*, two from Tertiary beds near Hobart, Tasmania and two from Vegetable Creek. Although these identifications may be correct, none have been substantiated by cuticular study. Truswell *et al.* (1985) regard small tricolporate pollen grains from the Oligocene-Miocene Oakvale-1 corehole of the western Murray Basin, South Australia as being comparable to *Weinmannia*. The discovery of *Weinmanniaphyllum* macrofossils at Cethana therefore provides further evidence for the probable presence of *Weinmannia* in Australia during the Tertiary. Since *Weinmannia* is entomophilous and under-represented in pollen samples the presence of fossil pollen gives a reliable indication of the presence of *Weinmannia* forests. Similarly, an abundance of its pollen implies it was dominant. In Tertiary samples these small grains may often have been lost during preparation or overlooked by palynologists.

We are continuing with further study of this family. Although he was working before the widespread acceptance of plate tectonics theory, Bernardi (1963a) recognised the biogeographic interest of the Cunoniaceae and the paradox of the great distribution of *Weinmannia* in contrast to that of *Cunonia*, even though the similar seeds of these taxa would seem to have a similar poor dispersal. In particular, he suggested that there must have been an ancient dichotomy within the genus, since there are species of *Weinmannia* in Madagascar and the Mascarenes in the otherwise American section *Weinmannia*. Species in this section characteristically have pseudoracemes, an annular disc, a persistent calyx and compound leaves with a

winged petiole between the leaflets. On the other hand species of the Australasian-Pacific region characteristically have racemes, a disc consisting only of small non-functional glands alternating with the stamens and a caducous calyx. *Weinmannia* seeds can only be dispersed by wind (and fresh water) and they rapidly lose their ability to germinate (Bernardi 1963a). It is therefore likely that the current distribution of this taxon is largely a function of the break-up of Gondwana, and subsequent complex geological developments in the Pacific, whereby dispersal and establishment of propagules could only take place across minor barriers. In fact, I perceive that *Weinmannia* is a critical genus for enabling a comprehension of the biogeographic history of the Southern Hemisphere, in particular that of the geologically complex Pacific region. *Weinmannia* has an apparent preference for low latitude montane environments. Only a few species occur in temperate zones, though Wardle (1966) states that *W. racemosa* may be the most abundant tree species in New Zealand.

The fossils described here contribute little to the study of evolution within the family, but do demonstrate that these taxa had evolved by the Oligocene. Dickison (1984) disputes aspects of the existing taxonomy within the Cunoniaceae. For instance, he thinks that the diagnostic tightly packed globose inflorescence type of the three genera in the tribe Pancheriae evolved among diverse elements, citing numerous morphological differences between these genera. That is, he states that the xylem anatomy is quite variable, and there is both imbricate and valvate sepal aestivation, superior and inferior gynoecia, and dehiscent (*Callicoma*, *Pancheria*) and indehiscent (*Codia*) fruits producing seeds of quite different structure. However, cuticular features observed in this thesis suggest a very close affinity between *Codia* and *Callicoma*, and it is highly unlikely that their current similarity is purely the result of convergent evolution. There are about 20 species of *Codia*, many of which are restricted to New Caledonian maquis, or heathland on serpentine soils (Specht 1979). It is probable that *Codia* does have a common ancestry with *Callicoma* and may also have a long history of association with oligotrophic soils. A cladistic analysis of this family may be of great interest.

Order Fabales

Fabaceae

? ***Daviesia*** Smith

Specimen examined. C-464, 618

Description. These leaves are pinnatisect and up to 40 mm long with alternately placed apically directed lobes up to 7 mm long and with a decurrent base 5 mm wide, which is the point of maximum width (Figs 22a, b). The lobes taper to a mucronate tip in which a single prominent secondary vein terminates. C-618 seems to be two separate leaves which were apparently sessile, with gradually increasing sized lobes from the base. Cuticle is thick and well preserved on both specimens and is unequally amphistomatic with multiple partially formed stomates on the adaxial surface (Fig. 22c). Stomates on the abaxial surface occur in individual depressions (Fig. 23d) and are randomly aligned (Fig. 22e). There are typically four or five small subsidiary cells in a ring around stomates, and therefore these can be regarded as cyclocytic (Figs 22e, f). The nature of the guard cells is obscure but they appear to have been overarched by the subsidiary cells and have thick elongate cutin rims along the stomatal aperture (Fig. 22f). The outer walls of the subsidiary cells are thickened and furrowed radially. Apart from the stomatal depressions the abaxial surface is smooth whereas on the adaxial surface the outlines of the epidermal cells are marked by raised rims of cuticle (Fig. 22g). The anticlinal walls are thick. There is no evidence for the presence of trichomes or glands.

Discussion. Apart from certain Proteaceae, extant Australian plants with small pinnatisect leaves are few, and are apparently confined to the Leguminosae. Within this family a few Western Australian species of *Acacia* and *Daviesia* with a similar leaf or phyllode form were noted (Blackall and Grieve 1974) and the cuticles of *A. glaucoptera* and *D. pectinata* examined. The former species was clearly distinct from the fossil taxon in being paracytic whereas the cuticle of *D. pectinata* exhibits some similarity. In particular, although the guard cells are distinct (possibly because they are not sunken) from those of the fossils, the stomatal apparatus is quite similar in being cyclocytic (Fig. 22h, i) with thickened periclinal subsidiary cell walls (Fig.

Figure 22.

Figs a-g. ? *Daviesia* sp. (p.77)

a. C-464. Pinnatisect leaf. Scale: 5 mm.

b. Counterpart of **Fig. 22a** showing the mucronate lobes with prominent midvein traces. (Scale as for **Fig. 22a**).

c. LM of adaxial cuticle from C-618 showing partial stomatal development and thick anticlinal cell walls. Scale: 100 μm.

d. SEM of outer abaxial cuticle surface from C-464 showing a stomatal depression. Scale: 10 μm.

e. LM of abaxial cuticle from C-618 showing arrangement of stomates. Scale: 100 μm.

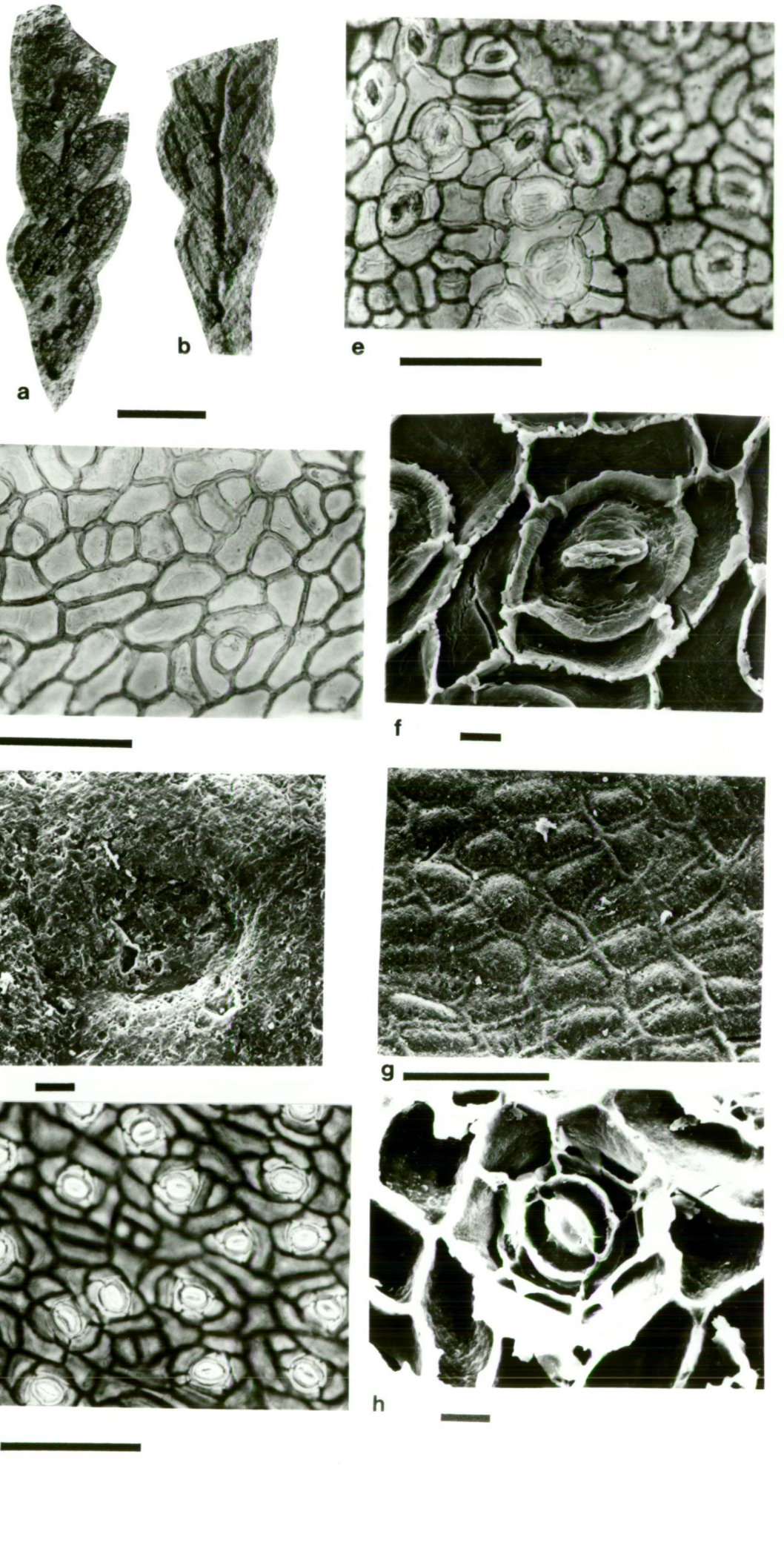
f. SEM of inner abaxial cuticle surface from C-464 showing a stomate. Scale: 10 μm.

g. SEM of outer adaxial cuticle surface showing cell outlines. Scale: 100 μm.

Figs h, i. extant *Daviesia pectinata*.

h. SEM of inner cuticle surface showing a stomate. Scale: 10 μm.

i. LM showing arrangement of stomates. Scale: 100 μm.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22h). However, *D. pectinata* is evenly amphistomatic, whereas the fossils have partially formed stomates on the abaxial surface. *D. trigonophylla* Meissn. has a similar leaf form but has yet to be obtained for comparison. Clearly, more investigation of cuticles is required to establish the precise relationships of the fossil taxon, although in the extant flora it is probably related to *Daviesia* species of Western Australia.

Another taxon in the Cethana flora with partially formed stomates on one leaf surface has already been discussed. This is *Acmopyle glabra*. Hill and Carpenter (1991-appendix I) also recorded a similar phenomenon in *Dacrycarpus* and suggested that it was a response to the development of more seasonal and cooler and drier climates. Fossils which may have affinity to *Daviesia* with partially formed stomates are therefore significant since this state was hitherto unknown in angiosperms. This indicates that if stomates are being lost from leaves of this taxon, then this phenomenon occurred in diverse groups, probably in response to the same environmental pressures. This species also provides additional evidence that scleromorphy and sometimes xeromorphy evolved in response to edaphic conditions. Extant *Daviesia* species with similarity to the fossil taxon occur in the sandy and lateritic soils of southwestern Western Australia associated with such genera as *Banksia*, *Dryandra*, *Grevillea*, *Macrozamia* and *Drosera*. The climate is Mediterranean. Many plants in this region, including *D. pectinata*, are amphistomatic (Pate *et al.* 1984). It was proposed by Mott *et al.* (1982) that the effect of developing stomates on the upper surface as well as the lower is to increase maximum leaf conductance to CO_2. These authors found a strong correlation between amphistomaty and plants with a high photosynthetic capacity, living in full-sun environments, and experiencing rapidly fluctuating or continuously available soil water - plants which would derive an adaptive advantage from a high maximum leaf conductance since they could grow rapidly in favourable conditions. Therefore, the possibility that the fossil species was increasing the number of stomates on the adaxial surface should not be dismissed, since such habitats probably occurred adjacent to the depositional site.

Order Proteales

Family Proteaceae

The Proteaceae is a clearly defined family with no close relatives and has long been recognised as significant to botanical research in the southern hemisphere. Johnson and Briggs (1975) published a major review and phylogenetic scheme for the family based on characters such as leaf form and sequence, chromosome number and size and the anatomy and morphology of the inflorescence, pollen, wood and fruit. In addition pertinent ecological considerations were made and the fossil record and biogeographic history of the family discussed. There is no doubt that the Proteaceae is an ancient Gondwanic family. Pollen is found from the late Cretaceous and provides some of the earliest evidence of Gondwanic angiosperms. Indeed, there is evidence that many of the first Proteaceae evolved in areas fringing the Late Cretaceous seaway between Eastern Antarctica and southern Australasia (Dettmann 1989). Such species include those with affinity to *Beauprea*, *Gevuina/Hicksbeachia* and *Knightia*. Affiliates of *Xylomelum* and *Macadamia* were also present in the Cretaceous of Antarctica but may have reached southern Australia from western Antarctica. This antiquity is now reflected in the basically southern hemisphere distribution of the family, and the fact that some genera, or sets of closely related genera, have widely disjunct distributions. Perhaps most striking are the presence of *Lomatia*, *Orites* and *Oreocallis* in Australia and South America, subtribe Gevuininae in Australia, New Guinea, the Pacific and South America and the very closely related genera, *Macadamia*, *Panopsis* and *Brabeium* in Australasia, South America and South Africa respectively (Johnson and Briggs 1975).

Most modern proteaceous taxa, including those of tropical rainforests, are sclerophyllous and Tertiary macrofossils and dispersed cuticles are abundant. However, a comprehensive assessment of cuticular features in the Proteaceae (which would facilitate fossil identification) has yet to be made, although Johnson and Briggs (1975), in summarising previous research, note that the family has characteristic paracytic stomates and trichomes which are found in all genera. Numerous records of proteaceous macrofossils from Australia were made in the 19th century and early in the

20th century by researchers such as Ettingshausen (1888), Deane (1903) and Chapman (1937). Lange (1978) studied Eocene dispersed cuticles from Western Australia and found that many were closely comparable to those of extant Proteaceae. Recently described macrofossils include leaves of many species allied to *Banksia* and *Dryandra* (Cookson and Duigan 1950; Blackburn 1981; Hill and Christophel 1988; Hill 1990b), Musgraveinae inflorescences from Victoria (Christophel 1984) and a *Banksia* cone from Western Australia (McNamara and Scott 1987). Blackburn (1981) also described *Maslinia grevillioides* from the Eocene Maslin Bay flora and suggested it should be placed in the tribe Grevilleae.

There was clearly a remarkable diversity of Proteaceae at Cethana. Apart from unidentified and probably extinct groups taxa have been referred to four of the seven tribes of the subfamily Grevilleoideae as recognised by Johnson and Briggs (1975). The modern affinities of these plants occur in a range of habitats from rainforests to sclerophyllous heathlands. Martin (1982) observes that in Palaeocene to mid-Eocene pollen assemblages from south-eastern Australia the Proteaceae is clearly the dominant angiosperm group but concommitant with a marked increase in *Nothofagus* pollen in the mid-late Eocene, many of these taxa declined and became extinct by the beginning of the Oligocene. Specht (1988) and Martin (1982) consider that with the extremely high rainfalls which occurred in the Tertiary, soils formed on predominantly quartz would have been even less fertile than today. The decline of the Proteaceae is as yet enigmatic, but may be related to the increase in vulcanism around the Eocene-Oligocene boundary, which markedly reduced the extent of nutrient poor soils.

Cuticles from species in 42 genera of the Proteaceae were examined using LM and sometimes SEM and compared to the fossil cuticles. Many taxonomically important characters have been recognised. These include the morphology of trichome bases, the alignment and distribution of stomates and the nature of cuticular surface ornamentation. In combination with aspects of the leaf morphology such as lobes or small marginal teeth, these characters have enabled the confident placement of many Cethana taxa into extant genera, occasionally with clear specific affinities. So far, 18 discrete macrofossil taxa have been recognised, most of them with well preserved

cuticle. Some of these taxa are described in detail and affinities suggested. The preliminary nature of most of these determinations should be recognised, but it is considered that there is great potential in using analysis of extant Proteaceae cuticles for identifying fossils. At this stage the major importance of the Cethana proteaceous taxa is in the remarkable diversity of species and the general high level of scleromorphy and in some cases obvious xeromorphy displayed. Of the taxa for which affinities are suggested, some are also of great biogeographic interest.

Cookson and Duigan (1950) examined the cuticular structure of species in the tribe Banksieae. This was the first major analysis of proteaceous cuticle and was undertaken in order to identify fossils from the Yallourn brown coals which they noted were similar to *Banksia* or *Dryandra*. The new genus *Banksieaephyllum* was erected to accomodate these forms, and six species recognised. Subsequently, several other species have been described from Early Eocene to Early Miocene deposits of south-eastern Australia, bringing the tally to 11 (Blackburn 1981, Hill and Christophel 1988). Hill and Christophel (1988) also erected the new genus *Banksieaeformis*, to encompass taxa which conformed architecturally to *Banksia* and *Dryandra*, but which lacked cuticle. Two species were described, including *B. dentatus* from Cethana. All of the *Banksieaephyllum* species so far described from the Early Tertiary of south-eastern Australia have superficial stomates, in contrast to the bulk of extant *Banksia* and *Dryandra* species (Blackburn 1981; Hill and Christophel 1988). This is interpreted as being a response to climate changes in the Late Tertiary which included developing aridity and particularly seasonality. In this thesis four new species of *Banksieaephyllum* are recognised, and one of *Banksieaeformis*. This diversity is comparable to that which may currently be found at sites only in south-western Western Australia or the Sydney sandstone region. Only two species of *Banksia* now occur in Tasmania.

Several *Lomatia* species are also present at Cethana. This genus has several species with distinctive relatively small pinnatisect toothed leaves. Four of the fossil taxa have such leaves and their cuticular morphologies support referral of these taxa to *Lomatia*. Similar pinnatisect leaves occur in several other genera of the subfamily

Grevilleoideae (Virot 1968; Johnson and Briggs 1975; Wrigley and Fagg 1989), especially *Grevillea,* but their cuticular characteristics are generally readily distinguishable. One species of *Lomatia* has been described formally (*L. xeromorpha*) and its foliage is almost identical to that of *L. tinctoria* ((Labill.) R. Br., a Tasmanian endemic shrub typical of fire prone dry sclerophyll vegetation (Carpenter and Hill 1988). Another species conforms closely to the north Queensland rainforest species, *L. fraxinifolia* F. Muell. The two other taxa exhibit an affinity to the genus, but not to any extant species. Unfortunately only two species of the South American genus *Roupala* could be obtained for comparison, and as this genus apparently contains species with similar leaves to *Lomatia* (Ettingshausen 1888; Johnson and Briggs 1975), these fossils cannot yet be assigned to *Lomatia* with certainty. Nevertheless, both of the *Roupala* species examined were clearly distinct from *Lomatia* on cuticular characters.

Another fossil leaf probably belongs to the subtribe Gevuininae of the tribe Macadamieae. This group is of great biogeographical interest, having closely related taxa in South America, New Caledonia, Vanuatu, Fiji, New Guinea and Queensland. Distinctively thickened trichome bases and an associated basal cell complex with a rim which appears serrated are apparently uniquely found on the abaxial leaf surface in species of this subtribe and the closely related Hicksbeachiinae.

Several other leaves possess proteaceous features and these are figured and briefly described.

Subfamily Grevilleoideae

Tribe Banksieae

Banksieaephyllum Cookson & Duigan

Banksieaephyllum sp. 1

Specimen examined. C-524

Description. This is a pinnately lobed leaf, 87 mm long and 24 mm wide, which is slightly incomplete at the base and apex (Fig. 23a). The alternately placed lobes are apparently present from base to apex, are directed at approximately right angles and have straight or convex apical sides and convex basal sides, with acute sinuses. The apex of these is slightly acuminate or mucronate (Fig. 23a, b). Secondary venation is craspedodromous with three distinct veins per lobe. Higher order venation is reticulate (Fig. 23b). The brachyparacytic stomates (Fig. 23c) are superficial within these reticulations (Fig. 23d). Trichome bases are abundant along veins and amongst the stomates. These are small, cylindrical and thickened. Larger trichome bases associated with up to four epidermal cells occur on the abaxial surface (Fig. 23e). The adaxial epidermal cells are small and isodiametric.

Discussion. In leaf architecture, there is a remarkable resemblance of this species to the extant south-western Western Australian species, *Banksia grandis* Willd. and *Dryandra drummondii* Meissn. (Fig. 23f). There are three other fossil taxa with a similar leaf form known from Eocene deposits in south-eastern Australia, *Banksieaephyllum incisum* (Blackburn 1981), *B. cuneatam* and *Banksieaeformis decurrens* (Hill and Christophel 1988). However, apart from the fact the lobes of the leaves of these species are apically directed, an important difference is that in these species the leaf base (where preserved) is drawn out or cuneate. This is a feature not found in extant *Banksia* and *Dryandra*, and therefore Hill and Christophel (1988) suggested that these species may have represented evolutionary dead-ends with no direct relationship to extant species. In fact, these *Banksieaephyllum* species may be more closely allied to subtribe Musgraveinae of the tribe Banksieae, which includes the north-eastern Queensland rainforest genus *Musgravea* (Christophel and Greenwood 1988; Christophel 1989). This seems likely since they occur in deposits

Figure 23.

Figs a-e. *Banksieaephyllum* sp. 1 (C-524). (p. 83)

a. Leaf. Scale: 10 mm.

b. Enlargement of **Fig. 23a**. Note the reticulate venation of the lobe on the right and the secondary veins. Scale: 5 mm.

c. SEM of inner abaxial cuticle surface showing a brachyparacytic stomate (guard cells aligned top to bottom). The cuticle is poorly preserved. Scale: 10 μm.

d. SEM of inner abaxial cuticle surface showing that the arrangement of veins and stomates. Scale: 100 μm.

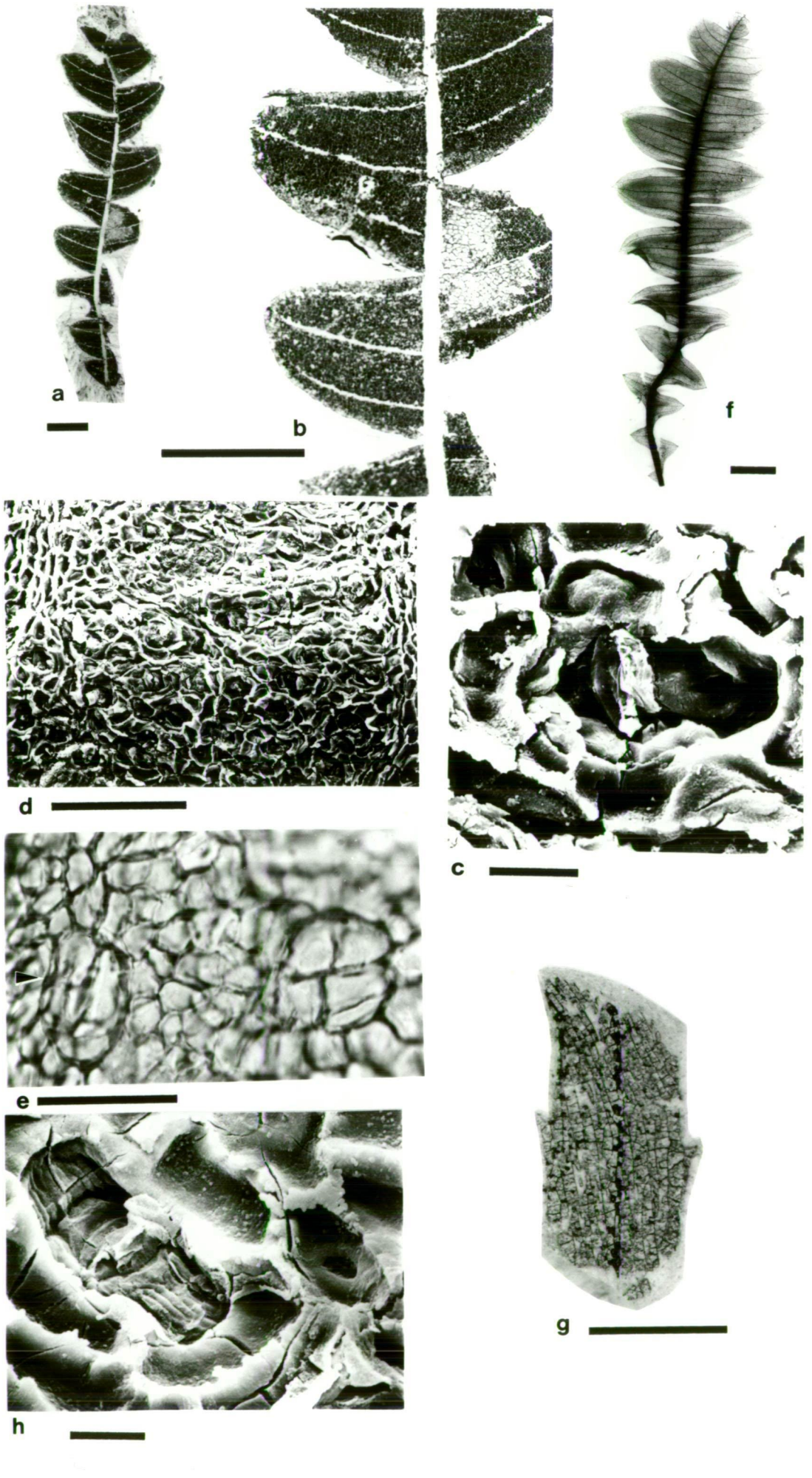
e. LM of adaxial cuticle showing small epidermal cells and two trichome bases (one is arrowed at bottom left). Scale: 100 μm.

f. Cleared leaf of extant *Dryandra drummondii*. Scale: 10 mm.

Figs g, h. *Banksieaephyllum* sp. 2 (C-624). (p. 84)

g. Specimen represented by a portion of a leaf with very small serrations. Scale: 10 mm.

h. SEM of inner abaxial cuticle surface showing a brachyparacytic stomate with prominently striated subsidiary cells and a trichome base at right. Scale: 10 μm.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apparently containing only rainforest taxa. The fact that the Cethana species has an identical leaf base (with lobes of decreasing size toward the base) to that of the group of pinnately lobed extant species including *B. grandis* is therefore significant, since it occurs with other highly sclerophyllous, probably non-rainforest taxa. It also demonstrates that this form had appeared by the Oligocene and was apparently present across southern Australia at least. The unequivocal presence of Eocene *Banksia* in Western Australia has already been established by McNamara and Scott (1983).

Banksieaephyllum sp. 2

Specimen examined. C-624

Description. The leaf compression is incomplete but clearly linear in form, being 6 mm wide and at least 33 mm long (Fig. 23g). The leaf and cuticle are thick. The presence of a few serrations at one end suggests this was the apical end of the leaf though it does not taper to either end. These serrations are only about 1 mm long and are apically directed with an acute sinus. The apical side is straight or concave and the basal side acuminate. Venation details are obscure, however the cuticle is well preserved. Stomates are of the typical *Banksia* form and appear to occur in shallow depressions between the minor veins on the abaxial surface. The lateral subsidiary cells are striated (Fig. 23h). The veins have numerous small, cylindrical, thickened trichome bases associated with one epidermal cell (Fig. 24a). These are also scattered among the stomates. The abaxial cuticle of an extant species, *B. spinulosa* Sm. is illustrated for comparison (Fig. 24b). No trichome bases have been observed on the abaxial surface of the fossil. This is composed of small, thick walled, approximately isodiametric cells with slight striations.

Discussion. This species is significant in that its leaf morphology is similar to *Banksia spinulosa* from eastern mainland Australia, one of the few species with occasional small serrations. Although the cuticle is fragmentary there is evidence that the stomates occurred in shallow depressions.

Banksieaephyllum sp. 3

Specimen examined. C-550

Figure 24.

(p. 84)

a. *Banksieaephyllum* sp. 2 (C-624). LM of abaxial cuticle showing arrangement of stomates and trichome bases. Scale: 100 µm.

b. Extant *Banksia spinulosa*. LM of abaxial cuticle showing arrangement of stomates and trichome bases. Scale: 50 µm.

Figs c, d. *Banksieaephyllum* sp. 3 (C-550). (p. 84)

c. Specimen represented by a portion of pinnately lobed leaf with one complete lobe at upper right. Scale: 1 mm.

d. LM of abaxial cuticle showing arrangement of stomates and trichome bases. Scale: 100 µm.

e. Extant *Dryandra formosa*. Scale: 5 mm.

Figs f-i. *Banksieaephyllum* sp. 4 (C-443). (p. 85)

f. Specimen; portion of serrate leaf. Scale: 5 mm.

g. SEM of inner abaxial cuticle surface showing a stomate. Scale: 10 µm.

h. SEM of inner abaxial cuticle surface showing that the stomates occur in areolar regions. Scale: 100 µm.

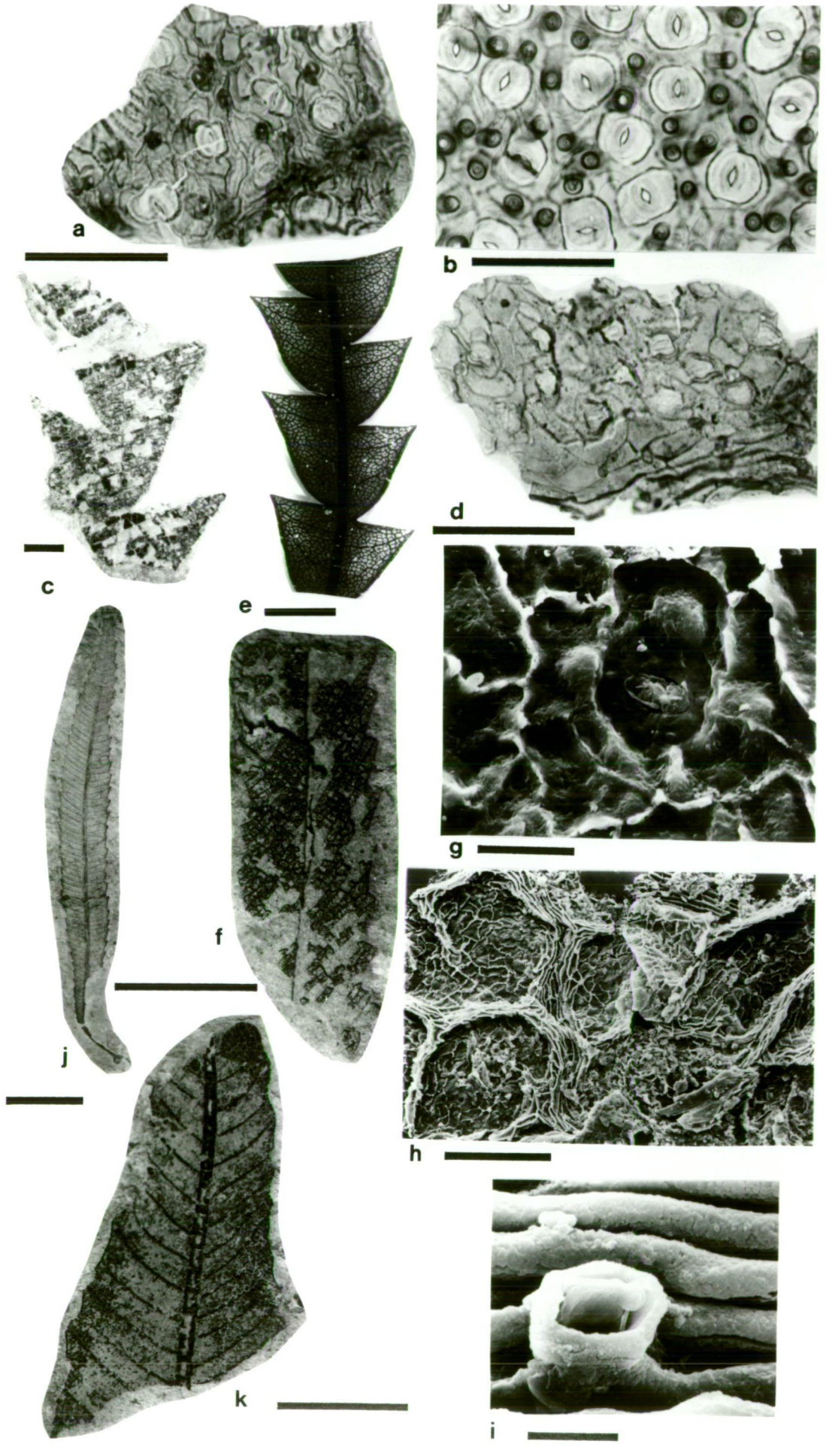
i. SEM of trichome base. Scale: 10 µm.

(p. 85)

j. *Banksieaeformis dentatus* (C-703). Note the attenuate leaf apex. Scale: 10 mm.

(p. 86)

k. *Banksieaeformis* sp. 2 (C-315). Scale: 5 mm.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Description. This is a portion of a pinnately lobed leaf about 20 mm long (Fig. 24c). The triangular lobes are about 2.5 mm wide and 4.5 mm long and apically directed. The apical side of the lobes is straight and the basal side is acuminate. No details of venation are distinguishable. The cuticle is thin and granular in appearance. The stomates appear to have been superficially situated in areas between vein reticulations on the adaxial surface (Fig. 24d). Unthickened trichome bases seem to be restricted to veins and occur at the ends of epidermal cells. No trichome bases were observed on the abaxial surface.

Discussion. In gross leaf morphology and size this specimen is very similar to *Dryandra formosa* R. Br. from south-western Western Australia (Fig. 24e), although the cuticle is clearly distinct. In any event no extant species of *Banksia* or *Dryandra* with small lobed leaves occurs in eastern Australia.

Banksieaephyllum sp. 4.

Specimens examined. C-443, 590, 630

Description. All specimens are incomplete in length, but the leaf width ranges from 6-13 mm. The specimens feature regular serrations at intervals of approximately 2 mm (Fig. 24f). These are straight or convex along the apical margin and convex basally, with acute serration sinuses. The secondary venation pattern is craspedodromous with one vein per serration. Intersecondary veins are prominent and common. The cuticle is quite thin. The stomates are brachyparacytic (Fig. 24g) and occur in the regions between vein reticulations (Fig. 24h). Unthickened trichome bases occur along the veins at the ends of the cells (Fig. 24i). No trichome bases have been observed on the adaxial surface.

Discussion. This species may be the cuticle bearing equivalent of *Banksieaeformis dentatus*, as its architecture and venation conforms to the description of this Cethana species by Hill and Christophel (1988).

Banksieaeformis R. Hill & Christophel

Banksieaeformis dentatus R. Hill & Christophel

Emended diagnosis. Leaf serrate, serrations acute. Apical and basal side of

serrations convex or straight, sinuses acute. Leaf base cuneate, apex attenuate. Leaf length approximately 60 mm, width 7-13 mm. Secondary venation pattern craspedodromous, one vein per serration. Intersecondary veins prominent, common.

Discussion. This species was described and discussed by Hill and Christophel (1988). The diagnosis is emended here because new specimens with the apex preserved have been recovered (Fig. 24j). Hill and Christophel note that the attenuate apex is unknown in extant species of *Banksia* and *Dryandra*, but it does occur in other fossil species allied to these genera.

Banksieaeformis sp. 2.

Specimens examined. C-294, 315, 711

Description. These leaves are up to 13 mm wide and estimated to be up to 55 mm in length. C-315 is illustrated in Fig. 24k. Serrations are small with a rounded apex and sinus. Secondary venation is craspedodromous with one secondary vein per serration. Several of these veins are forked. Intersecondary veins are prominent and directed at the sinuses where they form loops with adjacent secondary veins just inside the margin.

Discussion. This taxon has a similar margin type to *Banksieaephyllum attenuatum* from the Tasmanian Late Eocene Loch Aber deposit, which Hill and Christophel (1988) considered was similar to a number of extant *Banksia* species from eastern and western Australia.

***Discussion of* Banksieaephyllum *and* Banksieaeformis.** The Cethana deposit contains much evidence for interpreting the development of important elements of the Australian flora. In regard to leaves of the *Banksia/Dryandra* type the following points are made; 1) The diversity of species was high. For taphonomic reasons the tally of at least six taxa must be taken as only a fraction of the possible number occurring in the region. 2) Extant species with nearest architectural similarity to the fossils occur in both eastern and western Australia. 3) Stomates of the four *Banksieaephyllum* species are superficial; they do not occur in deep pits, although

trichome bases are abundant. These facts strongly suggest that the high diversity of species which occur in the Sydney sandstone flora and particularly in south-western Australia can be seen as a relictual situation, and not necessarily the result of recent speciation. Hopper (1979) discussed several reasons for the high level of endemism in this region of Western Australia and there is no doubt that the survival of relictual forms could be associated with the presence of ancient deeply weathered soils. Very similar *Banksia/Dryandra* forms to those now restricted to Western Australia persisted in Tasmania at least until the Oligocene.

Among extant species of *Banksia* and *Dryandra*, the presence of stomates in deep depressions is interpreted as a clear adaptation for limiting water loss (e.g. Hill 1990c). None of the *Banksieaephyllum* species so far described from sediments older than Late Oligocene (Latrobe Valley) exhibit this feature, although many, including specimens from Cethana, have very sclerophyllous small leaves with hairy surfaces. These are also characters which can be termed xeromorphic. This may be interpreted as evidence for developing seasonal aridity at Cethana, or perhaps more likely (given the abundance of associated obligate rainforest taxa), the presence of variably drained sites imposing a variety of water stress levels.

Tribe Embothrieae

Subtribe Lomatiinae

Lomatia R. Br.

Lomatia xeromorpha Carpenter & R. Hill

Specimen examined. C-217

Discussion. This specimen was described, illustrated and discussed by Carpenter and Hill (1988).

Lomatia aff. ***fraxinifolia*** F. Muell.

Specimens examined. C-495, 551, 556

Description. The first two specimens are similar in gross morphology, but C-495 lacks the apical portion of the leaf and C-551 the base. Each is about 50 mm long and 15 mm wide. The leaf apex and base are acute. There are at least 20 teeth around

the margin, each about 1 mm long and forming an acute angular sinus. The teeth are straight on the apical side and convex basally. No venation details are discernable. C-556 is evidently the pinnatisect tip of a leaf (Fig. 25a). One of the two leaflets is well preserved and 45 mm long with 10 teeth. The leaf is hypostomatic. The randomly arranged stomates are typically paratetracytic and feature pronounced T-pieces of cuticle at the poles of the guard cells (Fig. 25b, c). The cell walls are variably sinuous, a character most evident in C-556 (Fig. 25b). Occasional proteaceous trichome bases with usually two-to-three basal cells occur along veins and on the adaxial surface. The outer cuticular surface on the abaxial side is relatively smooth (Fig. 25d).

Discussion. The cuticular preservation of the fossils is excellent. The available evidence from foliar and cuticular morphology indicates that this taxon is closely comparable to *L. fraxinifolia* of north-eastern Queensland, a species which occurs in rainforests at altitudes over 1000 m (Wrigley and Fagg 1989), usually on granitic or sedimentary substrates. This species usually has bipinnate leaves although the leaflets may be pinnatisect (Fig. 25e). Cuticles from several leaves were examined and some variation in the degree of sinuosity or buttressing of the cell walls was observed. The outer abaxial surface is relatively smooth (Fig. 25f) compared to other species of *Lomatia*, but is very similar to that of the fossils. In fact, in all respects the cuticle of the fossils and that of *L. fraxinifolia* (Figs 25f-h) are virtually indistinguishable, suggesting a close affinity between these taxa.

Figure 25. *Lomatia*

Figs a-d. *Lomatia* aff. *fraxinifolia.* (p. 87)

a. C-556. Scale: 10 mm.

b. LM of abaxial cuticle from C-495 showing arrangement of stomates. Scale: 100 µm.

c. C-495. SEM of inner abaxial cuticle surface showing a stomate. Scale: 10 µm.

d. C-495. SEM of outer abaxial cuticle surface. Scale: 100 µm.

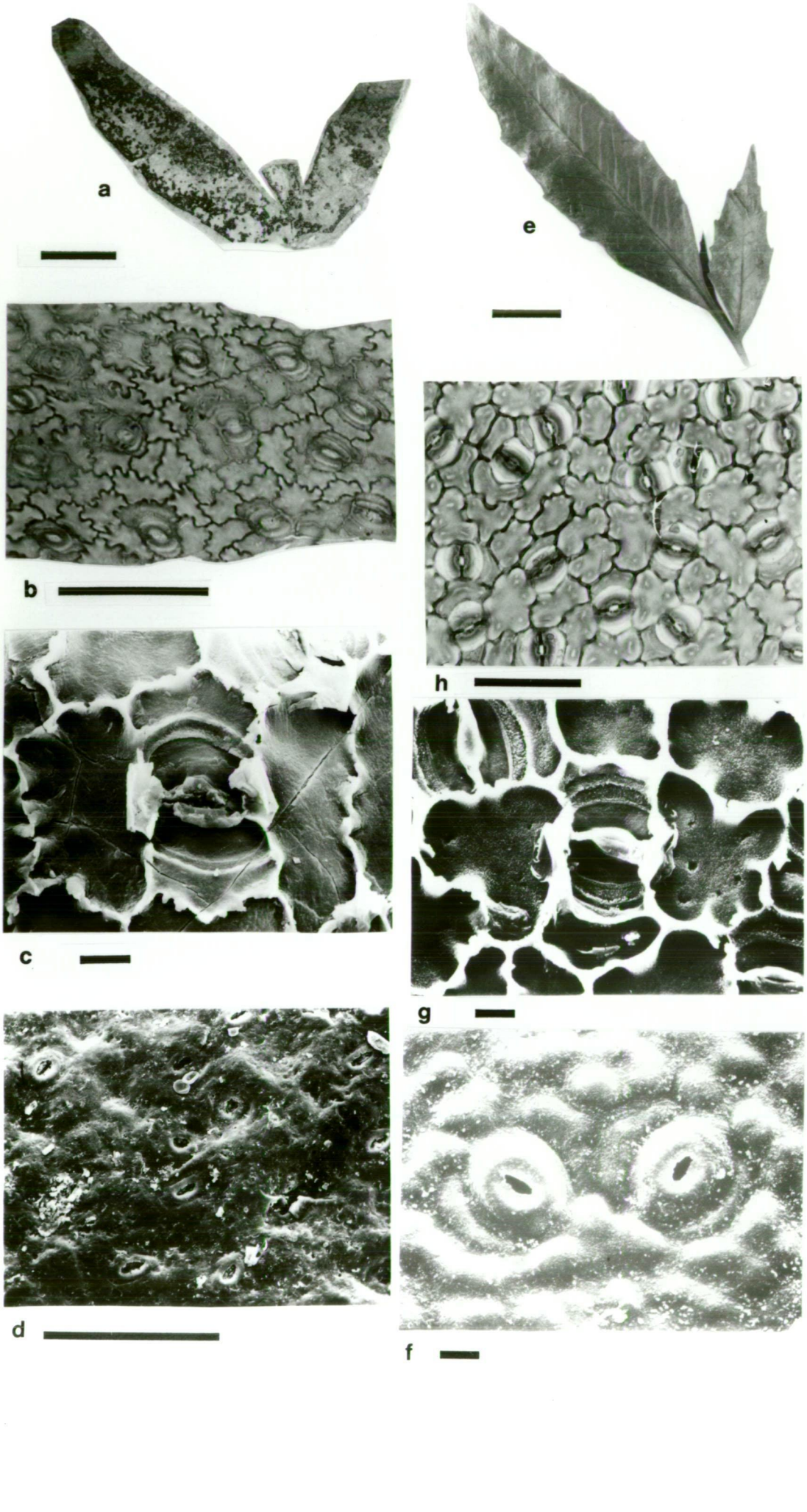
Figs e-h. Extant *Lomatia fraxinifolia.*

e. Leaflet from pinnatisect leaf. Scale: 10 mm.

f. SEM of outer abaxial cuticle surface. Scale: 10 µm.

g. SEM of inner abaxial cuticle surface showing a stomate. Scale: 10 µm.

h. LM of abaxial cuticle showing arrangement of stomates. Scale: 100 µm.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Lomatia sp. 3

Specimens examined. C-037, 442

Description. C-037 is an impression fossil composed of five leaflet pairs of a pinnatisect leaf, with distinctive reticulate venation. It was described and illustrated by Carpenter and Hill (1988). C-442 is a compression fossil which lacks vein preservation but is otherwise morphologically identical to this specimen (Fig. 26a). In particular there are about six prominent serrations along the apical margin of each leaflet and only one near the apex on the basal side. The leaflets are each about 16 mm long. The leaf is hypostomatic. The cuticle is quite thick and possesses numerous one-to-four celled trichome bases on the adaxial surface (Fig. 26b). Many epidermal cells on the abaxial surface also have associated trichome bases (Fig. 26c). The stomates are randomly oriented, typically paratetracytic (Fig. 26d) and feature raised crescentic rims of cuticle over the guard cell regions (Figs 26e). The epidermal cells are small and isodiametric with quite sinuous cell walls (Figs 26b-d).

Discussion. The leaf morphology and cuticle of this taxon shares many characteristics with *Lomatia*, though not with any one extant species. Carpenter and Hill (1988) noted a similarity of the impression fossil to forms of the eastern Australian species *L. fraseri* R. Br. and *L. silaifolia* (Sm.) R. Br. and the Chilean species *L. ferruginea* (Cav.) R. Br. The features of the abaxial cuticle of C-442 are very similar to that of *L. fraseri* of New South Wales (Fig. 26f, g), but the adaxial surface is clearly distinct from that of *L. fraseri* and is most similar to that of *L. ferruginea* (Fig. 26h).

Lomatia sp. 4

Specimen examined. C-629

Description. This species is also represented by what is evidently a pinnatisect leaf (Fig. 27a). The compressed leaf is very thick but only primary veins can be traced. One decurrent leaflet is clearly discernable and is about 35 mm long and 8 mm wide with two prominent teeth along each margin. The leaf is hypostomatic. The adaxial cuticle is composed of thick walled epidermal cells (Fig. 27b, c) and numerous

Figure 26. *Lomatia*

Figs a-e. *Lomatia* sp. 3 (C-442). (p. 89)

a. Drawing of a leaflet from the compression of a compound leaf (too difficult to illustrate using photography). Scale: 10 mm.

b. LM of adaxial cuticle showing small epidermal cells and abundant multi-cellular trichome bases. Scale: 100 µm.

c. LM of abaxial cuticle. Note the thickened crescentic cuticular rims around the stomates. Scale: 100 µm.

d. SEM of inner abaxial cuticle surface showing a stomate. Scale: 10 µm.

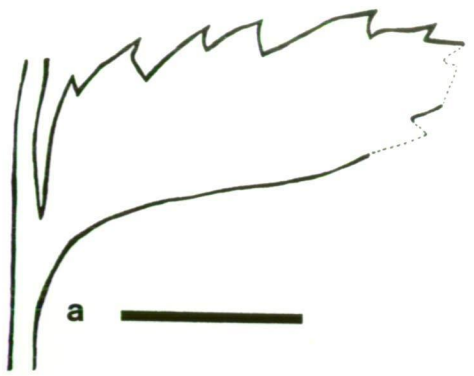
e. SEM of outer abaxial cuticle surface showing stomates and trichome bases. Scale: 10 µm.

Figs f, g. Extant *Lomatia fraseri.*

f. LM of abaxial cuticle showing stomates and trichome bases. Scale: 100 µm.

g. SEM of outer abaxial cuticle surface showing stomates and trichome bases. Note the thickened crescentic cuticular rims around the stomates. Scale: 50 µm.

h. Extant *Lomatia ferruginea.* LM of adaxial cuticle showing small epidermal cells and abundant multi-cellular trichome bases. Scale: 100 µm.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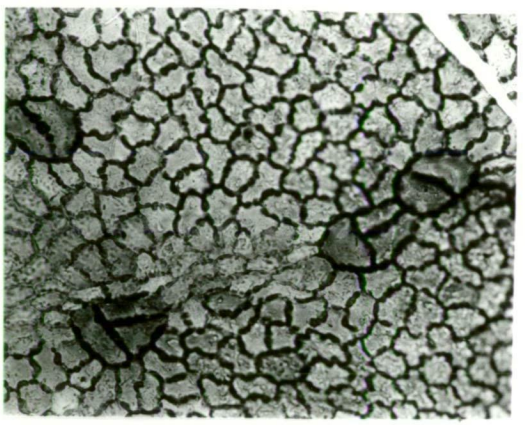
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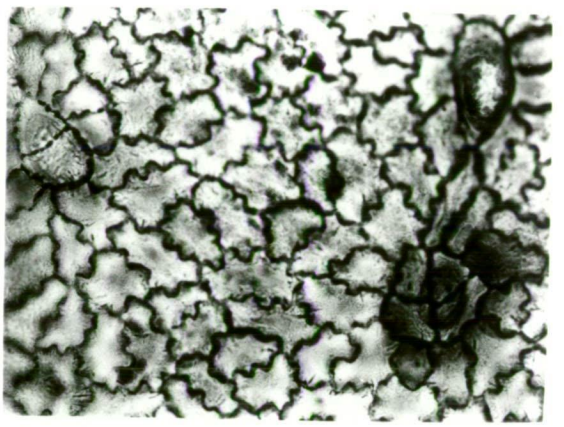
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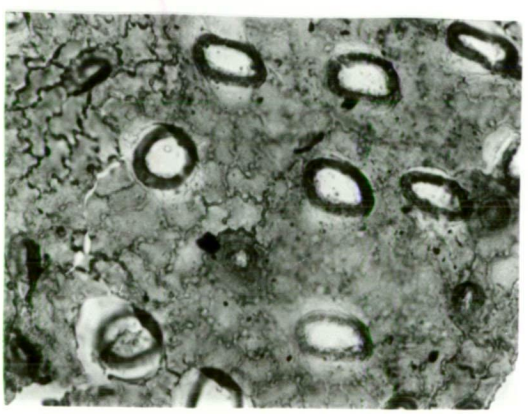
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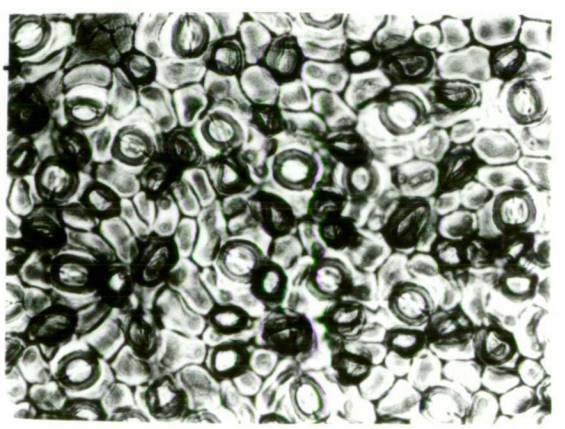
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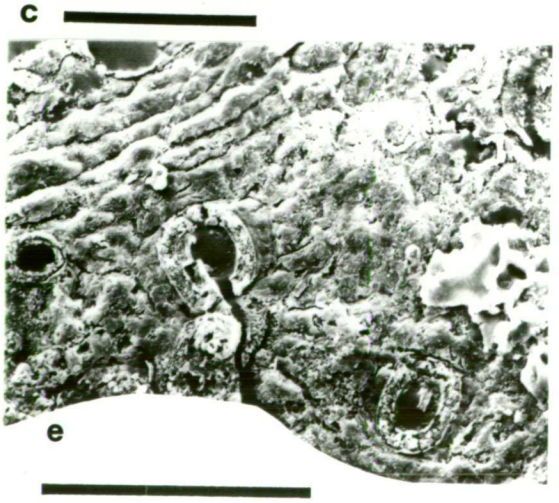
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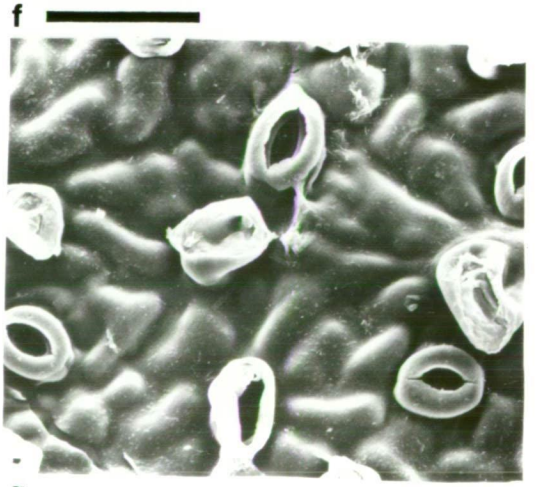
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Figure 27. Proteaceae

Figs a-e. *Lomatia* sp. 4 (C-629). (p. 89)

a. Specimen represented by a portion of a pinnatisect leaf. The segment at right has become detached near its base. Scale: 5 mm.

b. SEM of inner adaxial cuticle surface. Scale: 100 µm.

c. SEM of outer adaxial cuticle surface showing a trichome base. Scale: 50 µm.

d. SEM of inner abaxial cuticle surface showing a stomate (centre) and epidermal cells which each have associated trichome bases. Scale: 10 µm.

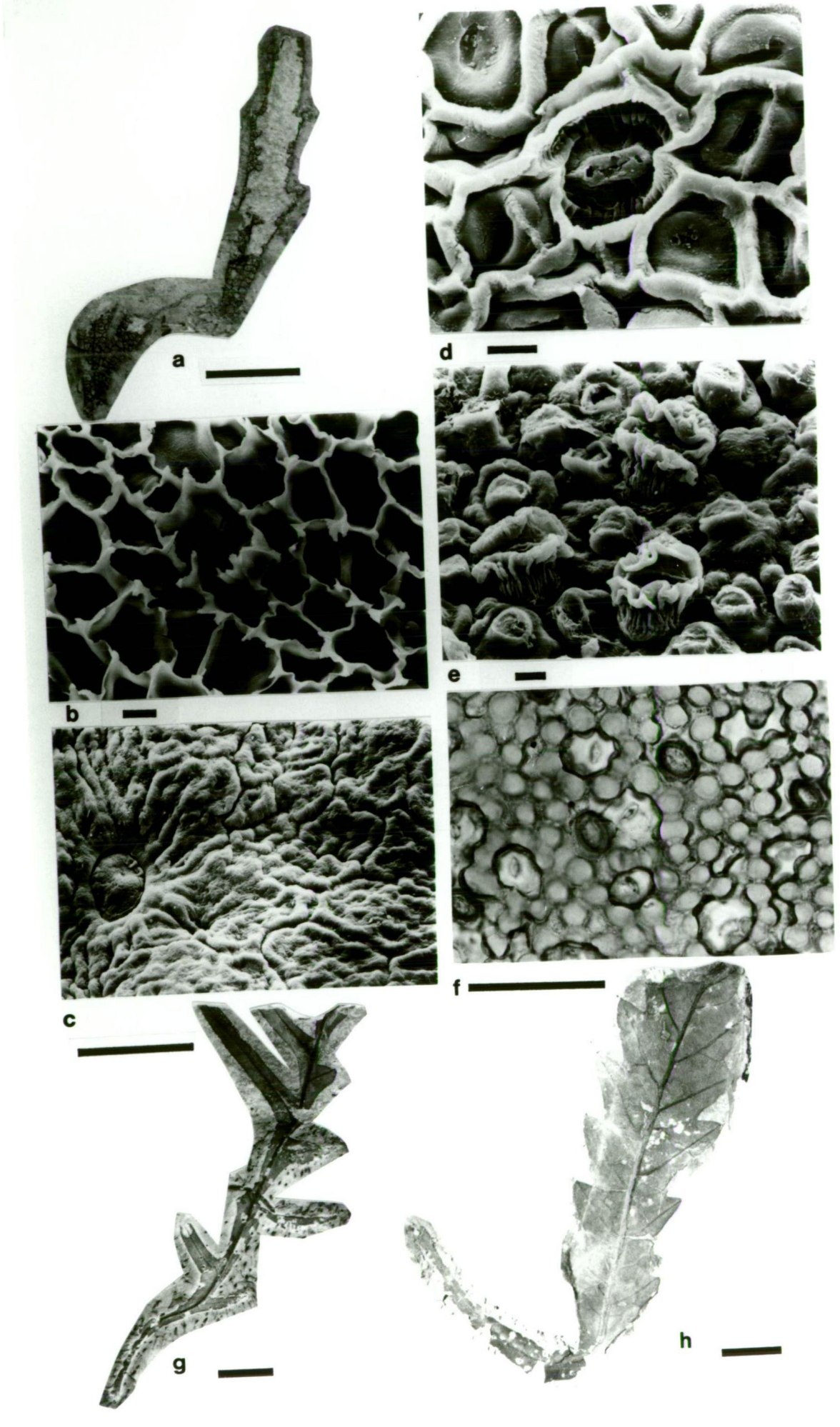
e. SEM of outer abaxial cuticle surface showing stomates with ornamented, raised undulate rims of cuticle and trichome bases. Scale: 10 µm.

f. Extant *Lomatia ferruginea.* LM of abaxial cuticle showing papillate surface sculpturing which partially obscures the stomates and trichome bases. Scale: 100 µm.

Figs g, h. ? *Grevillea* spp. (p. 90, 91)

g. C-714. Scale: 10 mm.

h. C-715. Scale: 10 mm.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trichome bases with multiple basal cells (usually eight). The stomates are paratetracytic (Fig 27d) and are enclosed to varying degrees by raised, undulate rims of cuticle (Fig. 27e). Each epidermal cell between the stomates has an associated trichome base (Figs 27d, e).

Discussion. This specimen is referred to *Lomatia* on the basis of the pinnatisect leaf form and cuticular characteristics, although there is no similar extant species. Preliminary study of *Lomatia* cuticles indicates that the adaxial cuticle of *L. dentata* (R. et P.) R. Br. of Chile is quite similar to that of the fossil, particularly in that there are small, thick cells and numerous trichome bases each associated with about eight epidermal cells. The peculiar cuticular lips over the stomates are unique, though *L. dentata* and *L. ferruginea* (Fig. 27f) also exhibit similar forms of protection for the stomates, in that the leaf surface has a thick papillate cuticle. Of all the Cethana taxa referred to the genus this one exhibits the most remarkable degree of scleromorphy and xeromorphy, and strongly suggests the plant was adapted to survival on sites with marked water stress.

Tribe Grevilleeae

A number of fossils have been recovered which are reminiscent of modern *Grevillea* species in details of leaf form and venation, but which lack cuticular preservation and have not yet been studied in sufficient detail to be certain of this affinity.

? ***Grevillea*** R. Br.

? ***Grevillea*** sp. 1

Specimen examined. C- 714

Description. This specimen is a pinnatisect leaf without cuticle (Fig. 27g). The alternately placed lobes are cut to almost the midvein and are variable in size and shape, ranging from triangular lobes about 6 mm long to narrow lobes 4 mm wide and up to about 30 mm long. The leaf is incomplete at the apex but is 90 mm long. There is only one secondary vein per lobe. A morphological similarity to extant species such

as *Grevillea banksii* R. Br. is noted.

? ***Grevillea*** sp. 2

Specimen examined. C- 715

Description. This craspedodromous leaf is about 110 mm long including a distinctive elongated leaf base (Fig. 27h). There are prominent serrations.

***Discussion of* Grevillea.** There are at least two other taxa which may have affinity to *Grevillea*, including C-536 and C-466, which have deeply lobed pinnatisect leaves. The leaves of some species of *Dryandra* have elongate lobes and are architecturally similar to these fossils, but *Dryandra* has more than one secondary vein per lobe, whereas in the two fossil taxa discussed here there is clearly only one. The presence of several *Grevillea*-like leaf forms at Cethana indicates that this genus, like *Banksia/Dryandra* was diverse in the Early Tertiary of Tasmania. These plants probably formed part of the same sclerophyllous communities. Currently, there are only one or two species each of *Banksia* and *Grevillea* in Tasmania compared to 75 species of *Banksia* and over 270 of *Grevillea* in mainland Australia (Wrigley and Fagg 1989). It is likely that these genera declined in Tasmania in response to the same environmental pressures, particularly the glaciations of the Late Tertiary and Quaternary.

Tribe Macadamieae

Subtribe Gevuininae

Specimens examined. C-569

Description. The leaf is shortly petiolate and slightly asymmetrical. The asymmetrical nature of the fossil suggests that it may have been part of a compound leaf. Although the apex is incomplete the length of the leaf is estimated to be 35 mm long and is 14 mm wide. Vein architecture is not discernable. The margin is sparsely toothed with short teeth about 5 mm long which form an acute sinus and which have a straight apical side and convex basal side. The leaf is hypostomatic. The cuticle is

Figure 28. Gevuininae

Figs a-d. C-569. (p. 91)

a. SEM of inner abaxial cuticle surface showing stomates and a multi-cellular trichome base at left. Scale: 10 µm.

b. SEM of inner adaxial cuticle surface. Scale: 10 µm.

c. LM of abaxial cuticle showing a trichome base and stomates. Scale: 100 µm.

d. LM of adaxial cuticle showing a multi-cellular trichome base. Scale: 50 µm.

Figs e-g. Extant *Turrillia vitiensis*.

e. SEM of inner abaxial cuticle surface showing stomates and a trichome base (arrowed at right). Scale: 50 µm.

f. SEM of inner adaxial cuticle surface. Scale: 10 µm.

g. LM of adaxial cuticle showing a trichome base. Scale: 100 µm.

h. Extant *Gevuina avellana*. LM of abaxial cuticle showing a multi-cellular trichome base and stomates. Scale: 100 µm.

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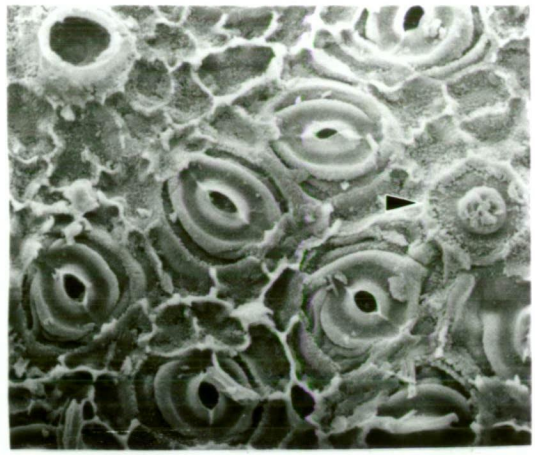

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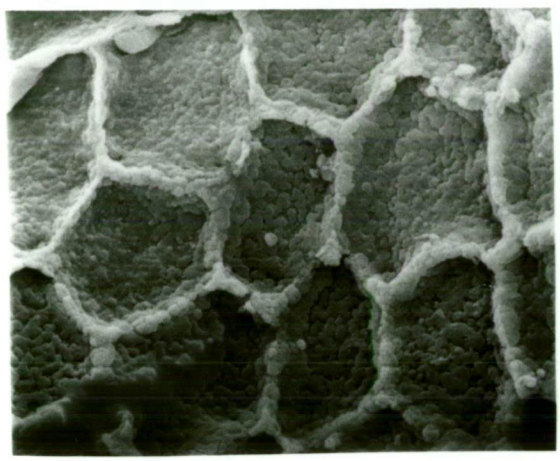

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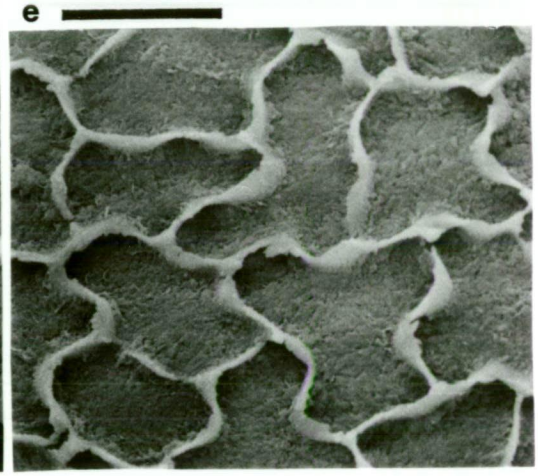

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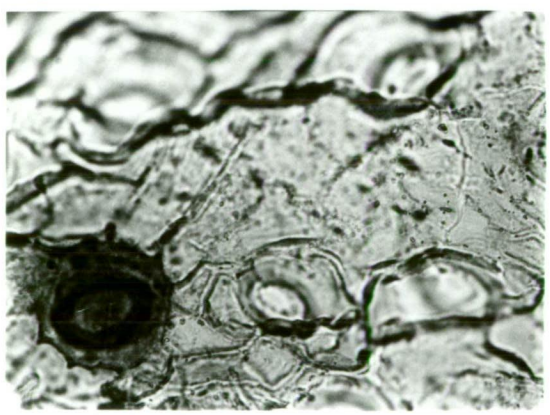

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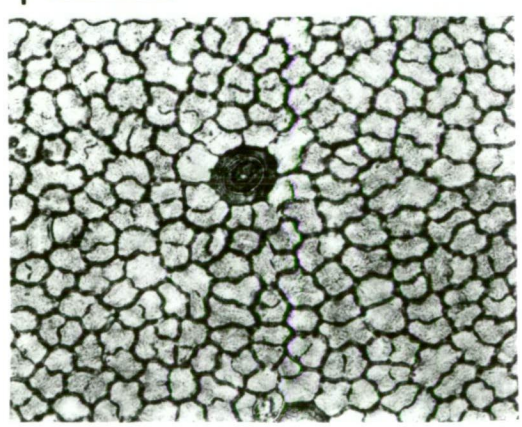

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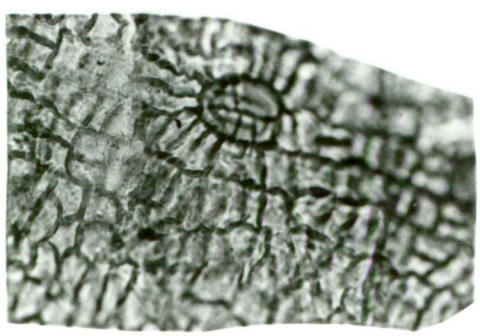

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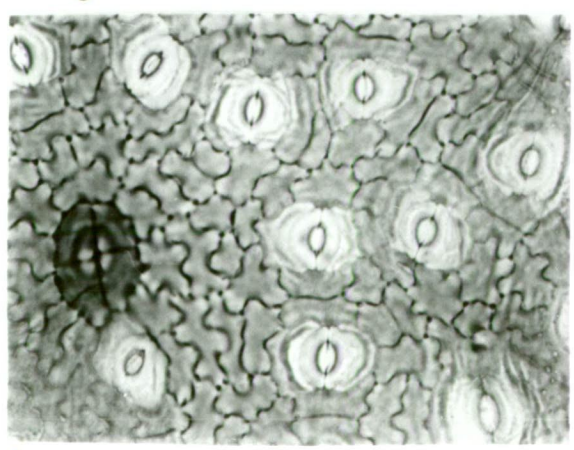

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thin and the outlines of the epidermal cells difficult to follow under LM. However, using SEM they are straight to slightly sinuously sided with granular walls (Fig. 28a, b). The randomly arranged stomates (Fig. 28a, c) are brachyparacytic and the lateral subsidiary cells are often striated. There are numerous rounded, thick (relatively heavily stained) trichome bases on the abaxial surface. There are one or two associated basal cells and these are also thickened and have a distinctive serrated outline (Fig. 28a, c). On the adaxial surface proteaceous trichome bases are abundant and may have up to eight basal cells (Fig. 28d).

Discussion. The available architecture and cuticular characteristics of this leaf strongly suggest an affinity to the subtribe Gevuininae. This is apparently composed of four genera (Smith and Haas 1975). These are *Turrillia* (Queensland, New Guinea, Vanuatu and Fiji), *Gevuina* (Chile), *Sleumerodendron* (New Caledonia) and *Euplassa* (South America). Unfortunately, no specimens of the latter could be obtained for comparison. However, the cuticular characteristics of the fossil match those of *Turrillia,* particularly *T. vitiensis* (Figs 28e-g) of Fiji and it is likely that this is where its affinities lie. This genus is composed of only five species, mostly restricted to upland rainforests (Smith 1985). Prior to the work of Smith and Haas (1975) the Australian and New Guinean species of *Turrillia* were included in the genus *Gevuina* with the Chilean species *Gevuina avellana* Mol. The evidence for a close relationship between these taxa based on gross morphological characters is supported by cuticular examination (Fig. 28h).

Proteaceae *incertae sedis*

Several other taxa can confidently be referred to the family. However, further research is required to determine their affinities more precisely, or whether they belong to extinct lines.

species 1

Specimen examined. C-219

Description. This leaf is incomplete at the base but is estimated to be 40 mm long and is 12 mm wide (Fig. 29a). The apex is acute and the margin is serrated with

Figure 29. Proteaceae

Figs a-d. C-219. (p. 92)

a. Specimen represented by a portion of a serrate leaf. Scale: 10 mm.

b. SEM of outer abaxial cuticle surface showing stomates and a trichome base (arrowed). Scale: 100 µm.

c. SEM of inner abaxial cuticle surface showing a stomate and a trichome base (arrowed at left). Scale: 10 µm.

d. LM of adaxial cuticle showing two trichome bases (at left two-celled and at right single celled). Scale: 100 µm.

Figs e-g. C-591. (p. 93)

e. SEM of inner abaxial cuticle surface showing a stomate and a trichome base (arrowed at left). Scale: 10 µm.

f. SEM of inner adaxial cuticle surface showing two multi-cellular trichome bases (arrowed). Scale: 50 µm.

g. SEM of outer abaxial cuticle surface showing a stomate and a trichome base (at left). Scale: 10 µm.

h. Extant *Hicksbeachia pinnatifolia.* LM of adaxial surface showing a multi-cellular trichome base and unevenly thickened anticlinal cell walls. Note the similarity to C-591 (**Fig. 29f**). Scale: 100 µm.

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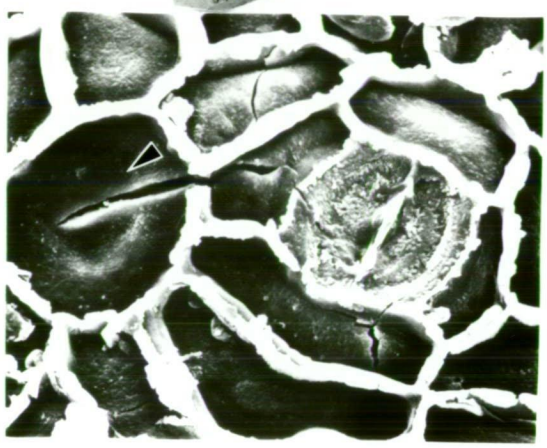
b



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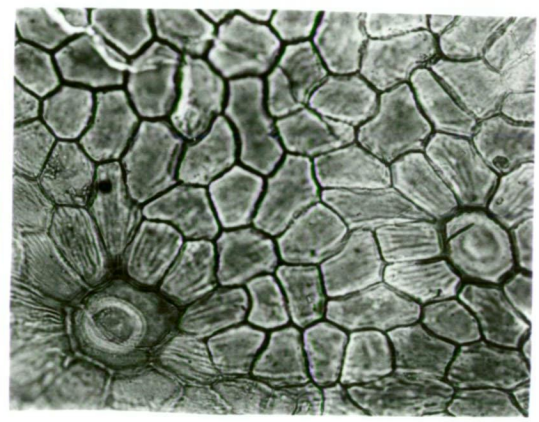

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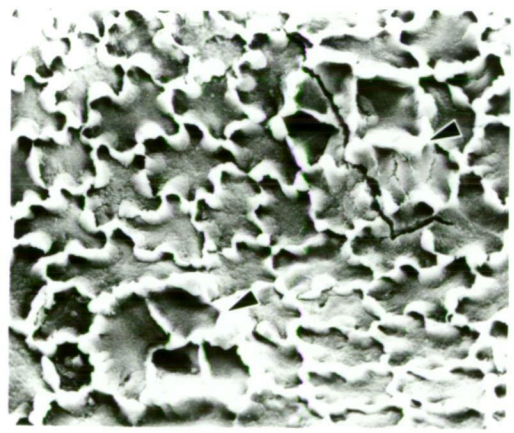

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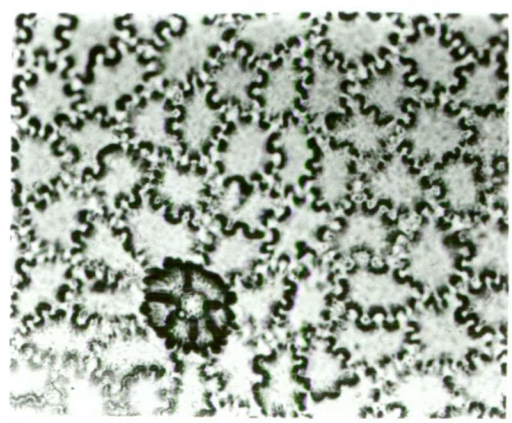

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1 mm long teeth. The leaf is hypostomatic and the cuticle is thick. The brachyparacytic stomates are randomly arranged and have raised crescentic rims of cuticle around the stomatal aperture (Fig. 29b). The cuticle of the guard and lateral subsidiary cells is noticeably granular (Fig. 29c). Numerous proteaceous trichome bases occur on both surfaces and are associated with one or two basal cells (Fig. 29b, d). The adaxial surface is prominently striated (Fig. 29d). The striations radiate from the trichome base cells.

species 2

Specimen examined. C-591

Description. This is a very thick leaf, incomplete at the base and apex, but tapering to both ends implies a length of about 70 mm. Its maximum width is only 9 mm. Very small sharp serrations about 0.5 mm long occur sparsely along the margin. They have an acute serration sinus and are straight along the apical side and convex basally. The cuticle is also very thick (Figs 29e-g) and the leaf is hypostomatic. The inner abaxial cuticular surface is markedly granular (Fig. 29e). The cell walls are unevenly and heavily thickened or buttressed (Fig. 29f) to give a sinuous appearance and the adaxial surface appears very similar to that of extant *Hicksbeachia pinnatifolia* (Fig. 29h). There are characteristic proteaceous hair bases on both surfaces (Figs 29e-g).

species 3

Specimen examined. C-571

Description. This specimen is 90 mm long and 13 mm wide and has a long tapering apex. The leaf base is incomplete but the leaf is estimated to be 110 mm long. The margin is regularly serrated with 0.5 mm long teeth. The leaf is hypostomatic. The abaxial surface has a distinctive irregular cuticular ornamentation (Fig. 30a) and the stomates have raised crescentic rims of cuticle and prominent T-pieces at the poles of the guard cells (Figs 30a, b). Proteaceous trichome bases are apparently restricted to the adaxial surface. These have one or two basal cells, and are surrounded by radial

Figure 30.

Figs a-c. C-571. (p. 93)

a. LM of abaxial surface. Scale: 100 µm.

b. SEM of inner abaxial cuticle surface showing two stomates. Scale: 10 µm.

c. LM of adaxial surface showing a trichome base and radial striations. Scale: 10 µm.

Figs d-f. C-567. (p. 94)

d. LM of adaxial surface. Scale: 100 µm.

e. SEM of outer abaxial cuticle surface showing a stomate. Scale: 10 µm.

f. SEM of inner abaxial cuticle surface showing a stomate. Scale: 10 µm.

(p. 94)

g. C-296. LM of abaxial surface showing a stomate. Scale: 50 µm.

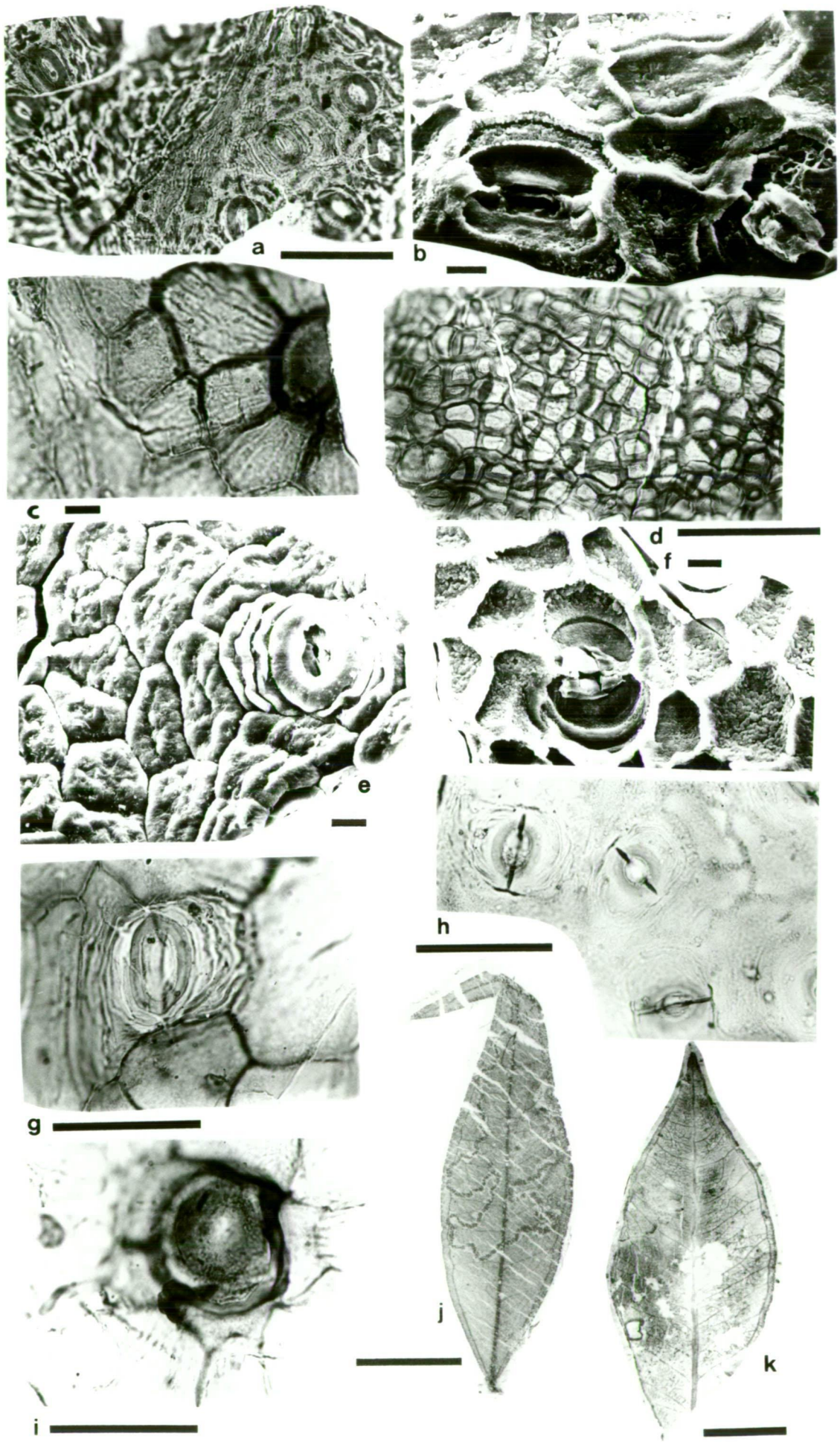
h. Extant *Helicia nortoniana* (F. M. Bail.) F. M. Bail. LM of abaxial surface. Scale: 50 µm.

i. C-296. LM of adaxial surface showing a trichome base. Scale: 50 µm.

Figs j-k. Myrtaceae leaves. (p. 95)

j. C-717. Note the leaf-mine. Scale: 10 mm.

k. C-718.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striations (Fig. 30c).

species 4

Specimen examined. C-567

Description. The specimen is incomplete at the apex but estimated to be 100 mm long and is 15 mm wide. Serrations are absent from the narrow basal third of the leaf. The small serrations are less than 1 mm long, form an acute sinus angle and are typically straight or convex on the apical side and convex on the basal side. The leaf is hypostomatic and the cuticle is extremely thick with small, thick walled epidermal cells on the adaxial surface (Fig. 30d). On the abaxial surface there are raised crescentic rims and pronounced lateral ridges of cuticle around the stomates (Fig. 30e), which mostly occur parallel to the long axis of the leaf. The stomates are brachyparacytic and the inner abaxial cuticle surface is markedly granular (Fig. 30f). Proteaceous trichome bases occur on both surfaces associated with two basal cells.

species 5

Specimen examined. C-296

Description. This specimen is an almost complete lanceolate leaf, about 60 mm long and 11 mm wide. The margin is serrated in the apical half to third with teeth about 1 mm long, forming an acute sinus angle. These teeth are straight on the apical margin and convex or acuminate along the basal margin. About 12 secondary veins terminate in the serrations. The leaf is hypostomatic. The cuticle is quite thin and the epidermal cells of the adaxial surface are masked by striations. Stomates are brachyparacytic and randomly arranged with crescentic striations on the lateral subsidiary cells (Fig. 30g) similar to that observed in species of *Helicia* (Fig. 30h). Trichome bases are thick (relatively heavily stained) and round and occur on basal cells which are also thickened. Surrounding the basal cells several small epidermal cells may occur (Fig. 30i).

Order Myrtales

Myrtaceae

Specimens examined. C-023, 029, 214, 306, 324, 350, 386, 393, 624, 716, 717, 718 and several others.

Description. The leaf size and shape are variable, from 11-48 mm long and 4-22 mm wide, and having a L:W of 1.7:1 -5.5:1. The leaf apex is obtuse, acute or attenuate and the base usually acute. All specimens have entire margins and brochidodromous venation with numerous secondary veins which arise at a high angle from the midvein and loop near the margin to form an intramarginal vein. Tertiary veins are random reticulate. Two specimens are illustrated (Figs 30j, k) but no specimen has been recovered with preserved cuticle.

Discussion. Christophel and Lys (1986) discussed the Tertiary record of myrtaceous macrofossils from Australia and proposed the organ genus *Myrtaciphyllum* to accomodate cuticle bearing leaves of the family which could not be assigned to any particular genus with confidence. They noted that leaves with a combination of lid cells, numerous high-angled secondary veins and an intramarginal vein were unique to the Myrtaceae. Microphyllous leaves of the Myrtaceae similar in architecture to several Cethana specimens were recorded from the Oligocene Pioneer deposit by Hill and Macphail (1983). The Cethana fossils lack cuticle and it is acknowledged that there are species of *Ficus* (Moraceae) with a similar leaf form to some of the Cethana specimens. However, it was considered that the possession of a continuous intramarginal vein and numerous high angled secondary veins was sufficient to refer the specimens to the family, in addition to the fact that Moraceae macrofossils are unknown in the Tertiary of south-eastern Australia, and have no pollen record until the Late Oligocene (in Victoria) (Luly *et al.* 1980; Truswell *et al.* 1987). Myrtaceae pollen has been recorded from Cethana. It is likely that at least two macrofossil species are present at Cethana, but Christophel and Lys (1986) have shown that leaf size and shape in the family is highly variable. Similar leaf types have been observed in numerous extant genera including *Syzygium*, *Metrosideros* and *Xanthomyrtus*. Specimen C-717 is of interest because it has the impression of long insect leaf mine (Fig. 30j). Rozefelds (1988) observed similar mines in several leaves

from the Eocene Anglesea deposit of Victoria which he considered were probably lepidopteran.

CHAPTER 5

CLIMATE

5.1 INTRODUCTION

It is often considered that there are essentially two, sometimes philosophically contradictory, approaches to the study of macrofossil floras, especially when the aim is to interpret past climates. One technique relies on fossil floristics where the past climate is inferred from the ecological preferences of the nearest living relatives. The other is independent of taxonomic procedure and is based on foliar physiognomy, where the climate is inferred from modern demonstrable relationships between leaf size and margin type and (especially) temperature and rainfall. Spicer (1990) recently reviewed a floristic (and palaeoclimatic) study of the Oligocene Creede Flora, Colorado by Axelrod (1987) and drew attention to the fact that in a physiognomic study of the same flora Wolfe and Schorn (1989) had come to quite different conclusions as to the estimated mean annual temperature at the time of deposition. Clearly, there should be congruence between the methods. As I have stated previously the most rigorous approach must be to consider all available evidence, and this includes not only floristic and physiognomic characters but also such information as that provided by plant surface features (such as cuticle morphology and epiphyllous fungi), sedimentology, palaeogeography and palaeoclimatology.

5.2 FLORISTICS

Extrapolation of past climate from the ecological range of modern species with close affinity to the fossil taxa depends upon accurate identification of the fossils. Apart from taxonomic errors the greatest problem with this approach is that an extinct species from a formerly diverse genus may have had a much different ecological range to the few extant relictual species of that genus. In the world's extant flora this is of greatest relevance for gymnosperms, a group which has obviously declined during the Tertiary. For instance, if *Araucaria araucana* (Mol.) K. Koch which is unique in the Araucariaceae in being restricted to very cold conditions (at the tree-line in Chile with deciduous *Nothofagus*) were extinct, then fossil leaves of that species,

though they are recognisably distinct from all modern species, may be presumed to have been derived from a plant growing in a much warmer climate. In addition, there is always the possibility that the ecology of extant species with closest affinity to unidentified taxa may be different to a general picture based on the ecology of the identified taxa. Notwithstanding the potential problems, I emphasise the importance of the fact that in this study over 20 macrofossil taxa have been identified to generic level, and of these several have very close inferred affinity to individual extant species. Furthermore, the identification of most of these taxa is based on cuticular examination, which lends great rigour to the accuracy of the interpretations.

Aspects of the ecology of the extant rainforest species with nearest affinity to the fossil taxa identified have been discussed in Chapter 4 and it was concluded that with very few exceptions these affinities lie in what could be described as low latitude montane or high latitude regions of the southern hemisphere. Rainforests of these regions, which include areas of New Guinea, New Caledonia and other Pacific Islands, New Zealand, Tasmania, mainland eastern Australia and Andean South America are usually dominated by *Nothofagus* and 'austral' gymnosperms, and typically include a mixture of other so-called Gondwanic elements such as members of the Monimiaceae, Proteaceae, Myrtaceae, Elaeocarpaceae, Cunoniaceae and certain Lauraceae. These forests are characterised by an abundance of mosses, lycopods, lichens and ferns which often occur as epiphytes. Although these regions may be separated by many degrees of latitude and longitude, certain climatic features appear to be shared between them. Stated simply and qualitatively the climate is cool with continuously high levels of rainfall and humidity (frequently a factor of persistent cloud cover at high altitude). Examples of quantitative assessments and estimates of mean annual precipitation (MAP, mm) and mean annual temperature (MAT, °C) for widely varying localities supporting rainforest vegetation with floristic similarity to that of Cethana are given in Table 5.1 as follows;

Table 5.1 Rainforest site data

Site	latitude	alt. (m)	MAP	MAT	Source
Sumac Rd, Tasmania	41° 09' S	180	1646	11.3	Hill *et al.* (1988)
New England, New South Wales	30° 30' S	1560	2149	9.6	"
Eastern Cordillera, Colombia	5° N	2900	2500	10	Grabandt (1980)
Puerto Montt, Chile	41° 28' S	13	1996	11.1	Veblen *et al.* (1981)
Wabag, New Guinea	5° S	1980	3015	16.7	McAlpine *et al.* (1983)
Hokitika, New Zealand	42° 30' S	39	2940	11.3	Wardle *et al.* (1981)
Mt Humboldt, New Caledonia	22° S	1640	4000	13.5	Schmid (1981)

These figures can be used to provide an indication as to the nature of the climate at Cethana at the time of deposition. It is important to note that the occurrence of evergreen rainforest is dependent on the absence of drought. For instance, the minimum precipitation limit for *N. cunninghamii* in Tasmania is about 1250 mm, including at least 50 mm per month during summer (Jackson 1965).

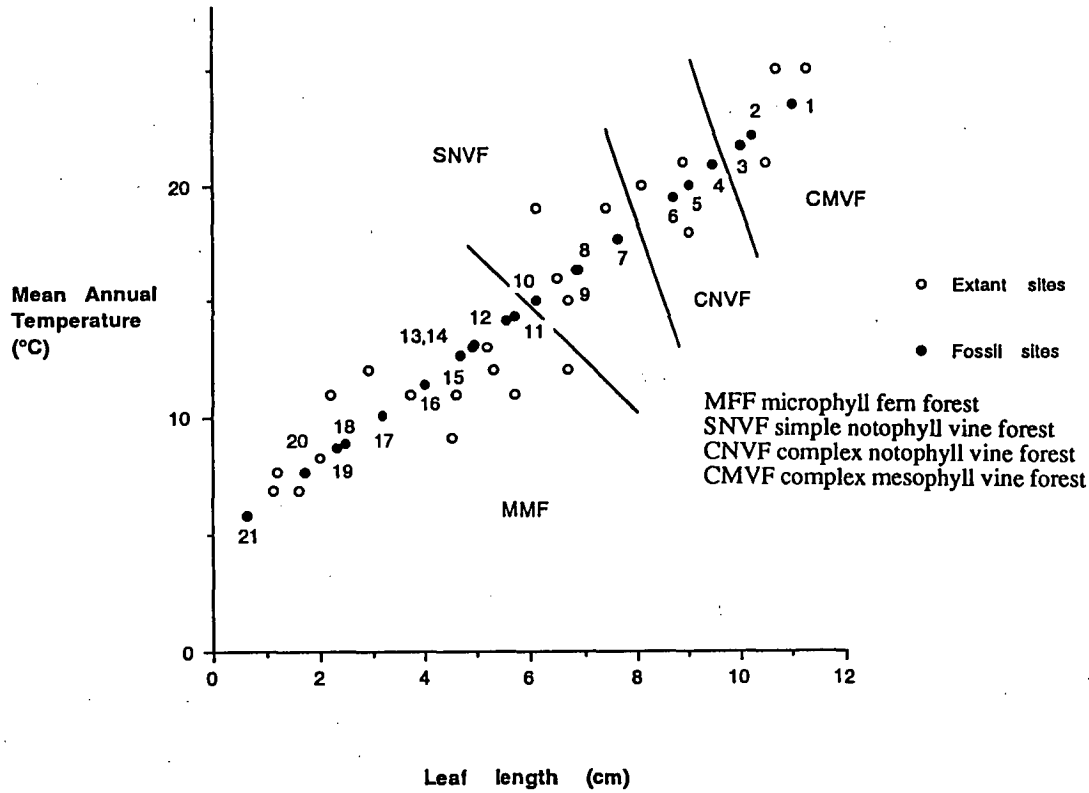
The affinities of many of the Cethana sclerophyllous elements are considered to lie in non-rainforest 'heathland' vegetation best represented in the Sydney sandstone region and in south-western Western Australia. The climate of the latter region in particular is Mediterranean, where essentially the winters are cool and wet and the summers are hot and dry. However, as I have discussed, the cuticular morphology of these species indicates that drawing climatic inferences from the ecological preferences of these nearest extant species may be less clear than for the rainforest element, since, as exemplified by *Banksieaephyllum* the stomates of the fossils are superficial or only slightly sunken, whereas those of most extant species occur in deep hair-filled pits. This suggests that the climate under which the modern species grow is much less mesic and the protection of the stomates is often related to extreme summer water stress. This highlights the precision which cuticular study can lend to climatic interpretations.

5.3 PHYSIOGNOMY

Foliar physiognomic analysis utilises assessments of leaf parameters such as size, shape and margin type and is therefore independent of taxonomy (e.g. Wolfe

Fig. 5.1. Plot of leaf length vs mean annual temperature (MAT) for extant and fossil sites (Hill, Carpenter and Jordan, unpublished data).

At each of several eastern Australian rainforest sites litter was sampled using the method of Greenwood (1987b). For each site, as well as for those studied by Greenwood (1987b), the mean value of leaf length was calculated. For each site MAT was obtained by using climate surfaces derived by M. F. Hutchinson (e.g. Hutchinson and Bischof 1983) as implemented in BIOCLIM Version 2.0, written by J. R. Busby (e.g. Busby 1988). The mean leaf length at each fossil deposit was superimposed over the line of best fit for the extant sites.



1 = Anglesea "Mesophyll Lens" (Christophel *et al.* 1987)
2 = Nerriga
3 = Maslin Bay (Christophel & Blackburn 1978)
4 = Lake Bungarby
5 = Anglesea (Christophel 1981)
6 = Maslin Bay (Christophel & Greenwood 1989)
7 = Golden Grove (Christophel & Greenwood 1987)
8 = Brooker
9 = Regatta Point
10 = Anglesea B (D.R. Greenwood pers. comm.)
11 = Anglesea A (D.R. Greenwood pers. comm.)
12 = Anglesea C (D.R. Greenwood pers. comm.)
13 = Vegetable Creek
14 = Anglesea D (D.R. Greenwood pers. comm.)
15 = Anglesea E (D.R. Greenwood pers. comm.)
16 = Loch Aber
17 = Cethana
18 = Pioneer
19 = Little Rapid River
20 = Lea River
21 = Monpeelyata

1971, 1979, 1990; Dilcher 1973; Dolph 1978; Christophel and Greenwood 1989). Leaves are obviously the principal organs of plant interaction with the atmosphere, and are therefore sensitive to prevailing environmental conditions, especially temperature. Thus, for example, there is no doubt that in general leaf size decreases as latitude and altitude increase. Also, it has long been known that lowland tropical rainforests have a greater percentage of taxa with entire margined leaves than those of temperate regions, although the adaptive significance of this is unclear (e.g. Bailey and Sinnott 1916; Richards 1952; Givnish 1987). Recently, in Australia, Christophel and Greenwood (1989), based on Greenwood (1987b) have claimed to be able to recognise 'physiognomic signatures' of Tertiary leaf assemblages which match those of modern rainforest litter from different rainforest types as classified initially by Webb (1959). They have then inferred palaeoclimates by extrapolation from the climate under which the most similar living rainforest occurs. Hill and Carpenter (unpublished) have observed several flaws in this method as it has been used to date in the Australian context. In particular, it assumes that modern structural analogues of the past rainforests exist. In addition, extreme microphylls (especially *Gymnostoma* and certain gymnosperms) are not included in the analyses, there are certain taphonomic biases which are not considered and it may be impossible to be certain that the fossil assemblage represents rainforest litter. Instead, Hill and Carpenter (unpublished) conclude that at present the simplest and most reliable physiognomic character for interpreting climate is the mean value of leaf length. In this respect they found a high correlation ($r = 0.93$) between MAT and the length of leaves in leaf litter from numerous rainforest sites along the eastern coast of Australia. This graph (Fig. 5.1) is presented on the facing page.

267 angiosperm leaves from Cethana were examined and the following data recorded; leaf length (L), leaf width (W), L:W, point of maximum width from base (MW), number of serrations per non-entire leaf (S) and margin type (M) (Wolfe [1990] regards margin type to be generally the best single character for estimating MAT). The means for each measurement in millimetres and the percentage of entire margined leaves are presented in Table 5.2 below.

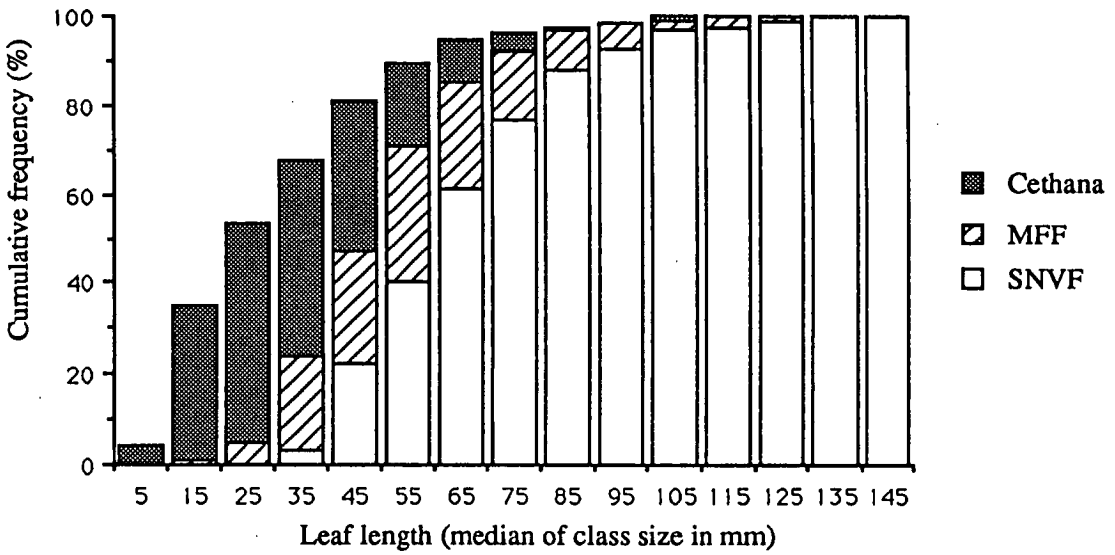
Table 5.2 Physiognomic data for Cethana leaves

L	W	L:W	MW	S	M
34	12	2.8	16	25	13 %

The mean length of leaves from many other south-eastern Australian deposits was calculated by Hill and Carpenter (unpublished) and is also provided on Fig. 5.1 which was described above. The measurements for Anglesea, Maslin Bay and Nerriga were derived from the data of the authors as acknowledged. From this graph, the estimate of the MAT for Cethana is 10.2 °C.

Subjectivity in the physiognomic analysis of Cethana leaves is considered to be minimal since all measurable leaves or portions of leaves in the collection were used and the specimens were collected at random. For compound leaves each leaflet was measured separately. Casuarinaceae and gymnosperms were not included in the analysis, because, although it is technically an arbitrary choice to ignore them, these taxa usually exist as stem sections or shoots with abundant extreme microphylls, and it was considered that this would bias the MAT estimate unacceptably. In contrast to the evidence for most angiosperms, it is unclear to what degree, if any, gymnosperm leaf size is related to environment. The difficulty in obtaining complete specimens from Cethana because of the uneven bedding is likely to bias the sample set to smaller leaves, and hence the MAT estimate is likely to be low. Perhaps the most pertinent point regarding the Cethana flora and the applicability of foliar physiognomic analysis *sensu* Greenwood (1987b) is that ample floristic evidence indicates that not all leaves in the deposit have been derived from closed rainforest. In addition, the relationship between edaphic factors and rainforest leaf physiognomy has not, as yet, been addressed in Australia. Nevertheless, it is clear that the Cethana flora is dominated by non-entire margined microphylls, and if the cumulative frequency for 1 cm size classes is plotted, the 'physiognomic signature' is closest to that of modern Australian microphyll fern forest (MFF) as determined by Greenwood (1987b) (Fig. 5.2 as follows).

Fig. 5.2. 'Physiognomic signatures' for Cethana, Microphyll Fern Forest (MFF) and Simple Notophyll Vine Forest (SNVF).
[Data for MFF and SNVF from Greenwood (1987b)].



It is also evident from Fig. 5.1 that the average leaf length for Cethana clearly falls within those measured from this type of rainforest. The *Nothofagus cunninghamii* dominated rainforests of Tasmania and Victoria and the *N. moorei* forests of north-eastern New South Wales are classified as MFF or microphyll mossy forest (MMF) as well as small regions of north-eastern Queensland above about 1000 m such as occurs on Mt. Bartle Frere and Thornton Peak (Webb 1959; Tracey 1982). Climatic records for these regions were discussed previously.

The fossil foliar organs from Cethana exhibit an extreme range of leaf and cuticular morphologies, from broad-leaf deciduous to markedly scleromorphic forms with highly reduced leaves. This is probably related to the presence of diverse habitats around the depositional site, where a mosaic of vegetation types existed in response to different levels of heat, light, water and soil nutrient availability. Very few specimens exhibit long acuminate apices or 'drip-tips' (these are mostly microphyllous Myrtaceae) and only one small leaf with a cordate leaf base has been recovered. The former are considered to be an adaptation to facilitate water drainage and hence discourage the growth of epiphyllous fungi (Richards 1952) and the latter

are typical of lianes (Webb 1959; Givnish 1987). Both leaf forms are most abundant in lowland tropical (megathermal) rainforests and their low proportions are consistent with the leaf size data which suggest a relatively cool environment.

5.4 EPIPHYLLOUS FUNGI

A total of 216 'germlings' were examined from Cethana cuticle preparations using light microscopy and each classified into one of the five grades recognised by Lange (1976). The results are presented in Table 5.3 below.

Table 5.3 Epiphyllous 'germlings' (% of total examined).

Grade 1	2	3	4	5 or 6
35	14	9	20	22

Lange found that the highest grade of 'germling' present could be used as an indicator of climate. In living vegetation Grade 5 or 6 forms indicate very wet conditions in which more than 1400-1500 mm of precipitation occurs annually. Furthermore, although not quantified, germling densities are high on cuticles from Cethana (as in numerous other Early Tertiary sites), indicating that very humid conditions prevailed. The potential for refinement of this approach is currently being investigated using an extensive range of modern and fossil sites. Preliminary investigations suggest that microsite effects may be more important than currently recognised.

5.5 PALAEOGEOGRAPHY AND PALAEOCLIMATOLOGY

These factors were discussed in Chapter 2.2 when the framework of the study was being established. It is reiterated that the major event of the Tertiary was the marked temperature decline at about the Eocene-Oligocene boundary, and that therefore this had occurred prior to the deposition of the Cethana flora.

5.6 CONCLUSION

There is clear congruence between the results of each approach considered as to the regional climate at Cethana at the time of deposition. The vegetation grew under continuously cool, humid, high rainfall conditions. Several authors have iterated that climates of the Early Tertiary probably have no modern analogue. However, Nix (1982) assessed past and present bioclimates for the Australia-New Guinea region and a major finding of his analysis was that "extensive areas with thermal environments favourable for each of the megatherm, mesotherm and microtherm elements have persisted on the evolving land mass of Terra Australis throughout the past 150 million years" and this has "permitted continued existence of conservative, slowly evolving stocks that shared a common inheritance in the Gondwanan land mass". It is particularly notable that Nix classifies a type of environment of the New Guinea highlands as mesotherm/microtherm nonseasonal, with a MAT of 12-14 °C. This 'Tumbunan' bioclimate is now restricted to regions which have much floristic similarity to Cethana, and supports numerous genera which are now extinct from Australia. It is also pertinent that the only regions in Australia where topography and climate combine to provide environments suitable for micro-, meso- and megatherms in close proximity are in the Macpherson-Macleay Overlap of north-eastern New South Wales and south-eastern Queensland (Burbidge 1960) and the ranges of the Atherton to Cape Tribulation region of Queensland.

The potential to obtain more precise bioclimatic information for several south-eastern Australian Tertiary fossil deposits is being investigated (Hill, Carpenter and Jordan, unpublished data). Local and microclimatic factors critical to plant distributions which cannot be determined with any confidence at present include the degree of seasonality of rainfall, diurnal and seasonal temperature ranges (? incidence of frosts), the degree of cloudiness and atmospheric CO_2 concentration.

CHAPTER 6

RECONSTRUCTION OF THE VEGETATION

6.1 TAPHONOMIC CONSIDERATIONS

Major reviews of plant taphonomic research have recently been written by Ferguson (1985) and Spicer (1989a). This aspect of research is not discussed in detail here but it may be of particular importance for understanding the Cethana deposit considering the apparent heterogeneity of the local vegetation. Interpretations of fossil floras in terms of community reconstruction are faced with a complexity of taphonomic and ecological problems. Although some generalizations about the make-up of Australasian fossil leaf beds have recently emerged from botanical taphonomic research based on modern examples (e.g. Drake and Burrows 1980; Hill and Gibson 1986b; Greenwood 1987b; Carpenter and Horwitz 1988-appendix II), it must the emphasised that no two depositional scenarios will ever be the same, and the Cethana site, based on what has been determined from geological interpretation, is probably extremely complex. Nevertheless, there is much evidence from these and more extensive studies from the northern hemisphere (e.g. Spicer 1981; Spicer and Wolfe 1987) to support the following salient points regarding lacustrine deposits. The vast proportion of macrofossils are derived from plants directly surrounding or overhanging the lake or inflowing streams and long distance transport of macro-plant organs should generally be disregarded. In addition, the vegetative material which reaches a depositional site has been derived from all synusiae of the surrounding vegetation. At Cethana it seems an extra dimension should be emphasised, that of input from plants growing to an unknown height above the lake on steep slopes and on a ridgeline. Casual observations below such cliffs demonstrate mixtures of leaves from these taxa (which in Australia are often sclerophylls) with those from species growing at the cliff base. The assemblage of macrofossils from Cethana comprises vegetative and reproductive structures from ferns, conifers and angiosperms. The overall tally of taxa so far recognised is at least 9 pteridophytes, 3 cycads, 15 conifers and 80 angiosperms. Most taxa are represented by one or at most a few specimens, suggesting a highly mixed assemblage derived from a highly diverse local flora,

including some input from inflowing streams. This is consistent with the expected scenario for lake deposits (Spicer 1981, 1989a; Wing 1987). It also suggests that many more taxa can be expected to be recovered with further study, and that the regional flora was also extremely diverse.

Usually the presence of morphological (especially cuticular) characters provides important independent data for determining the habitat of the plant in question. As discussed previously, the fossil foliar organs exhibit an extreme range of leaf and cuticular morphologies, from broad-leaf deciduous to markedly scleromorphic forms with highly reduced leaves. At one end of the spectrum of possibilities is that these plants grew under identical climatic (and microclimatic), edaphic, and light conditions, had organs with an equal potential for fossilization (considering such factors as life habit, phenology, physical and biochemical structure and dispersal) and grew in a more or less uniform spatial arrangement with respect to each other. Clearly, assuming uniformitarian principles this is highly unlikely to have been the case. Instead, it is emphasised that the depositional site was anything but a uniform physical environment and the fossil flora is composed of heterogeneous elements from a variety of habitats. Further, a component of the vegetation surrounding the site may have been in a seral state, following for instance a mass disturbance due to a landslip. This would also contribute to the heterogeneity of the local flora, and the fossil assemblage.

A study of the taphonomy and spatial distribution of macrofossil taxa within the deposit is beyond the scope of the present study. However, preliminary qualitative observations indicate that there are certain differences between the floras of the different depositional regions discussed in Chapter 2.1 which may be of significance in interpreting the vegetation surrounding the lake. For instance, the compound *Weinmanniaphyllum* leaves are quite common in the cream coloured finely laminated sediments with alternating sand layers of the southern inlier but have not been observed elsewhere. Conversely, no *Gymnostoma*, *Agathis* or *Banksieaephyllum*/*Banksieaeformis* leaves have been recovered from these sediments. However, taxa such as *Nothofagus tasmanica*, *Papuacedrus australis*,

Lomatia, *Dacrycarpus*, *Podocarpus* sp. 1, ? cycad, small leaved Myrtaceae and *Araucaria* sp. 1 definitely occur in both, although their proportions vary.

Although there are some clear similarities between the macro- and microfloral components there are also some clear differences, and some of these can be related to taphonomic factors. These discrepancies highlight the importance of a combined macro-microfossil study. The diversity and taxonomic make-up of pteridophyte spores and gymnosperm pollen is similar to that of the macrofossil taxa of each group recovered, but the estimated tally of at least 80 angiosperm macrofossil taxa is not matched by angiosperm pollen, where less than 40 taxa are recognised. *Nothofagus* and gymnosperms dominate the pollen assemblage and also are represented by abundant macrofossils. These are generally large trees with high productions of wind dispersed pollen (e.g. Luly *et al.* 1980), so it is not surprising that their pollen swamps that of other taxa. Macrofossils of *Nothofagus* are referrable to three of the four extant subgenera recognised by Hill and Read (1991) and the pollen to corresponding groups (Dettmann *et al.* 1990). This is in contrast to the situation in several south-eastern Australian mid-Eocene deposits reported by Christophel (1989) where *Nothofagus* pollen is common but there is an apparent lack of macrofossils, and strongly indicates that the genus was locally abundant at Cethana. In terms of abundance *Nothofagus tasmanica* leaves are the most common macrofossils, accounting for about 12 % of all angiosperm leaves recovered.

There are numerous other taxa for which there are occurrences of both macro- and microfossils. These include Casuarinaceae, Myrtaceae, Araucariaceae, *Dacrycarpus*, *Podocarpus*, *Dacrydium*, *Phyllocladus*, Blechnaceae, Cyatheaceae, Schizaeaceae and Gleicheniaceae. There is no doubt that all of these taxa formed part of the local flora at least.

Probably the low angiosperm pollen diversity compared to that of macrofossils can be attributed to the local presence of numerous animal pollinated and/or low habit species, in addition to the low taxonomic resolution and poor preservation of certain taxa. Here, the example of the Lauraceae is well known. Most of the tricolpate and tricolporate species cannot be identified, though the diversity of these forms does not

nearly match that of the angiosperm macrofossils. In terms of macrofossil diversity the Cunoniaceae and Proteaceae were very important families at Cethana but pollen of the former has not even been recognised while the pollen diversity of the latter does not nearly match that of the macrofossil taxa. While these discrepancies may generally be due to poor pollen preservation, the Proteaceae situation is in remarkable contrast to that observed in Early Tertiary (particularly Palaeocene to Late Eocene) deposits of south-eastern Australia, where the pollen diversity far exceeds that of the macrofossils (Martin 1982; A. R. H. Martin 1982). For instance, Christophel (1989) notes that the Anglesea site has more than 20 pollen species ascribed to the Proteaceae, but only three macrofossil taxa. The Cethana situation is virtually a reversal of this and must be at least partly related to the unusual nature of the depositional site already described. The most similar extant species of many of the Cethana taxa often have a low shrub habit (*Banksia*, *Dryandra*, *Lomatia*, and *Grevillea*), so normally there would be a low likelihood of pollen grains and vegetative matter reaching the depositional site by air currents. Possibly, as discussed in Chapter 2.1 a local land disturbance resulted in quartzitic gravel and leaves of these plants being dumped in the lake. Nevertheless, it is still remarkable that no pollen which can be referred to the Banksieae (*Banksieaeidites* spp.) has been recorded. All Proteaceae are animal pollinated (Johnson and Briggs 1975), and it is likely that the forms which became extinct during the Eocene were produced by dominant plants growing away from the waterside, so that fallen leaves would have a low potential for fossilisation.

6.2 COMMUNITY ECOLOGY

The type of vegetation and its stability at any given site is, and presumably has always been, a complex interaction between climatic, topographic and edaphic factors, as well as historical influences. The taxonomic affinities and physiognomic attributes of the Cethana fossil leaves have been established and it is evident that not only are the most similar extant plants distributed across a wide latitudinal range, there is a mixture of sclerophyllous (and even xeromorphic) taxa with mesic

rainforest taxa. Superficially at least, it seems somewhat incongruous that such a diversity of species should co-occur in the same deposit. Few Australian macrofossil deposits have been studied in sufficient detail or taxonomic accuracy to detect this phenomenon, but there are numerous examples from deposits of similar age to Cethana in the northern hemisphere which have been discussed by many authors. For instance, mixtures of taxa which have nearest living relatives now widely distributed both latitudinally and altitudinally in a variety of forest types have been documented by MacGinitie (1969), Dilcher (1973) (and numerous papers cited by him), Axelrod (1987, 1988) and Wolfe and Schorn (1989). Axelrod (1988) and Spicer and Wolfe (1990) have emphasised that there is a body of taphonomic evidence which indicates that these species were growing very close to the depositional sites, and did not include large input from remote high altitude sites. Instead, the apparent migration of these taxa (or retreat into small relictual centres) is largely attributed to the effects of subsequent climatic vicissitudes, especially the change from equable conditions in the Early Tertiary to climates with a greater mean annual range of temperature and precipitation, factors most pronounced during the Quaternary glaciations. Plants thus were 'sifted' relatively unchanged into climatic zones retaining the more equable conditions; moved into new regions and environments for which they were genetically predisposed; evolved morphological and physiological features which enabled them to survive the changing conditions; or whole phylogenetic lines became extinct. It should be recognised that although plant communities are not temporally stable associations of species, the uniformitarian assumption that the environmental requirements of fossil taxa should be more or less retained by their nearest living relatives must be adopted in palaeobotanical research, as for instance discussed by Read *et al.* (1990). In south-eastern Australian Tertiary deposits admixtures of apparently temperate and tropical pollen species are familiar to palynologists but because of differing pollen/spore dispersal and production this does not necessarily mean that these taxa were closely associated in the vegetation. Macrofossil research offers much greater resolution, and there is now ample evidence that species which have nearest living relatives in regions of widely varying latitude

were indeed growing in the same forests. Townrow (1965a, 1965b) recorded an association of several podocarp genera having low latitude affinities with other conifer genera now restricted to cool or cold habitats in south-eastern Australia (*Microstrobos* and *Athrotaxis*) from the Early Eocene Buckland deposit in Tasmania. Hill (1990a) recently reviewed the data from several Tasmanian Late Eocene and Oligocene deposits which demonstrate mixtures of taxa having nearest living relatives in Tasmania, eastern mainland Australia, New Guinea and elsewhere. In terms of its rainforest taxa the Cethana macroflora has strong similarities to other Tasmanian deposits of similar age. For example, the Oligocene Little Rapid River deposit contains three subgenera of *Nothofagus* and species of *Araucaria*, *Agathis*, *Libocedrus*, *Dacrydium*, *Dacrycarpus*, *Podocarpus*, *Lagarostrobos* and *Phyllocladus*. Hill (1990a), Wells and Hill (1989b), Hill and Carpenter (1989-appendix II) and especially Read *et al.* (1990) have discussed the co-occurence of some of these taxa, particularly *Nothofagus* in terms of climatic (including photoperiodic), topographic and disturbance factors using studies of the ecophysiology and population dynamics of nearest living relatives. It seems reasonable to propose the presence of similar associations of plants at Cethana growing under similar environmental conditions as at Little Rapid River. However, the presence of the highly diverse sclerophyllous and xeromorphic element is unique to Cethana and therefore it is pertinent to relate this to the unique physiographic and edaphic setting outlined in detail in Chapter 2.1. It is suggested that these scleromorphic taxa grew on low nutrient sites and that the degree of xeromorphy was compounded by the influence of topographic factors such as steep slopes with their rapid drainage and marked differences in incident light (and heat) levels. The importance of edaphic factors in plant morphology, evolution and distribution is rarely considered or is regarded as being secondary to climatic influences in most northern hemisphere palaeobotanical research. For instance, in a review of physiological characteristics of land plants in relation to environment through time Spicer (1989b) does not even refer to the relationship between nutrients and cuticular characters. No doubt this is largely due to the apparent lack of any well developed assemblage of scleromorphs peculiar to very low nutrient soils in the

northern hemisphere, where the present more or less scleromorphic floras were derived by modification of subtropical woodland (Johnson and Briggs 1981). In Australia, by contrast, large regions of the continent are composed of ancient, deeply weathered substrates (e.g. Nix 1981, 1982; Specht 1981; Martin 1982; Beckmann 1983) which support sclerophyllous xeromorphic heathland vegetation containing diverse Myrtaceae, Proteaceae, Leguminosae and Epacridaceae. The fact that sclerophylls now dominate a large proportion of the Australian vegetation has led ecologists such as Webb (1969), Beadle (1966) and Specht and Rundel (1990) to conduct research on vegetation /soil relationships of the native flora and discuss the likely origin of sclerophylly (Johnson and Briggs 1975, 1981; Nix 1982; Specht 1981; van Steenis 1979). Much recent palaeobotanical research (Carpenter and Hill 1988; Hill and Christophel 1988; Hill 1990b) has provided support for the theory of Loveless (1961, 1962) and Beadle (1966) that very low soil phosphate concentrations in particular have led to the evolution and development of this type of xeromorph, and not climatic factors. Because of the lack of important nutrients these plants have a reduction in the number of cells formed and a reduction in the length of the internodes, resulting in low shrubby growth forms (Beadle 1981). The highly diverse Proteaceae of south-western Western Australia and the Cape region of South Africa exemplify this and are testament to a very long, probably pre-Tertiary history on oligotrophic soils. The possession of scleromorphic features preadapted certain taxa to the emergence of cold high latitude/high altitude conditions and seasonally hot and dry (Mediterranean) climates during the Late Tertiary, as well as increased fire frequencies. The degree of xeromorphy has probably been accentuated by these climatic factors so that apart from having thick cuticles, reduced leaves and the presence of hairs, some modern xeromorphs also have deeply sunken stomates and strongly revolute leaf margins. Many also display features such as woody fruits which enable them to survive fires. Beadle (1966) suggested that xeromorphic adaptations commenced at the margins of rainforests and evolved along gradients of fertility from high to low. *Grevillea*, *Lomatia* and *Orites* were cited as good examples of how this evolutionary scenario may have developed, since they all have species in

both rainforest and sclerophyllous vegetation. Several Cethana taxa are scleromorphic and some of these could have been rainforest taxa as discussed below. However, there are also taxa such as *Lomatia xeromorpha* (Carpenter and Hill 1988), *Macrozamia australis* (Carpenter 1991-appendix I) and *Banksieaephyllum* species which exhibit some degree of xeromorphy, with highly reduced leaves and/or well protected stomates and clear affinity to taxa which are now restricted to sclerophyll vegetation. Blackburn (1985) has also observed numerous such taxa in the Late Oligocene-Early Miocene Yallourn (Latrobe Valley) coal beds including *Callitris* (Cupressaceae), non-*Gymnostoma* Casuarinaceae, Epacridaceae and several species of *Banksieaephyllum*. The *Banksieaephyllum* species so far recorded from Cethana do not have the degree of protection of stomates as occurs in closely similar forms in the modern flora. However, two species of this genus from the Latrobe Valley have sunken stomates and recurved leaf margins, although there are species there which do not display obvious xeromorphy (Blackburn 1985; Hill 1990c). Therefore, it could be hypothesised that the increase in more xeromorphic forms was the result of broad-scale climatic deterioration. There is accumulating evidence for convergent foliar response to this in several other taxa (Hill and Carpenter 1991-appendix I). All evidence from the fossil record thus supports the hypotheses outlined above concerning the evolution of xeromorphy. The presence of obligate rainforest species at Cethana indicates that there was little or no water stress in terms of precipitation. However, it is hypothesised here that a diverse sclerophyllous element grew on nutrient poor and periodically anaerobic sites with a fluctuating water table on the lake margins. According to the habitats in which similar extant species typically occur such plants were several gymnosperms (especially *Agathis*, *Phyllocladus*, *Lagarostrobos* and *Dacrydium*), *Gymnostoma*, some *Banksieaephyllum*, *Gleichenia*, Restionaceae, *Drosera* and *Schizaea*. The more xeromorphic taxa occupied well drained sandy or rocky soils, probably with a strong northerly aspect. These sites had a more pronounced water stress and probably supported taxa such as *Macrozamia australis*, *Lomatia xeromorpha*, ?*Daviesia* and certain other species with affinity to *Lomatia*, *Banksia* and *Dryandra*. This element of the Cethana flora

provides some support for the evidence presented by Specht (e.g. 1981, 1989) that sclerophyllous vegetation evolved in seasonally waterlogged, infertile soil within a mesothermal climate.

Webb and Tracey (1981) have stressed that Australian rainforests also develop on very poor acid granite, sandstone and quartzitic substrates where soil texture and nutrient levels improve. Typically these forests include such plant families and genera as *Ceratopetalum* and other Cunoniaceae, Escalloniaceae, Winteraceae, Monimiaceae, Podocarpaceae, *Elaeocarpus*, *Nothofagus*, many Proteaceae and Lauraceae and in Australia retain a high degree of endemic taxa. Structurally, they are classified by Webb and Tracey (1981) and Tracey (1982) as Simple Notophyll and Microphyll Evergreen Vine Forests and Fern Forests. Their present day habitat is mostly in the cool, moist uplands of the Border Ranges of Queensland and New South Wales, and in montane areas of north-eastern Queensland, New Guinea and New Caledonia (Paijmans 1976; Johns 1982; Axelrod and Raven 1982; Whitmore 1984). Their diversity is apparently highest where very high rainfall and persistent cloudiness occur. Hyndman and Menzies (1990) suggested that these conditions compress ecological zonation to produce the extremely diverse biota they recorded for the lower montane rainforests of the OK Tedi headwaters of New Guinea. It is likely that lower altitude cloud cover occurred in the Early Tertiary in south-eastern Australia because of higher sea surface temperatures (Bowler 1982; Truswell et al. 1985). It is possible that in combination with its rugged topography, the altitude of the Cethana site was sufficient to enable the formation of persistent cloudiness.

Grubb (1974), Flenley (1979) and Whitmore (1984) refer to the fact that soils in many wet montane tropical regions suffer much leaching. There is strong evidence that the consequent oligotrophy of these soils has led to the selection of the sclerophyllous leaf form which predominates in these regions (Medina *et al.* 1990). Relatively high levels of exposure to strong winds and sunlight also seem to favour sclerophylly (Sugden 1985). However, despite having small coriaceous leaves these plants are relatively drought intolerant, indicating that sclerophylly in these regions is not related to water stress (Grubb 1974). It may be that many taxa which have a

taxonomic and physiognomic similarity to the species of these forests are well preserved in many Tasmanian fossil deposits because of their evergreen sclerophyllous leaves.

The identification of a diverse cunoniaceous element at Cethana is novel in the Tertiary fossil record and there is some ecological and biogeographical literature concerning the family which may be used to explain this. The Cunoniaceae are now usually associated with oligotrophic soils. Baur (1957), Floyd (1981) and Webb (1959) all note that *Ceratopetalum apetalum* and *Schizomeria ovata* D. Don may dominate warm temperate Simple Notophyll Vine Forest associations in New South Wales on poorer soil types such as those of sedimentary and granitic origin. The only extant Tasmanian representative of the family, *Anodopetalum biglandulosum* A. Cunn. ex Hook. f. or "horizontal" is restricted to the wetter regions of the state, usually on nutrient deficient Precambrian substrates (Jackson 1965). Apart from climatic and edaphic evidence, there are some data on rainforest population dynamics which may assist in understanding why *Weinmannia* became extinct from Australia. Studies of *W. racemosa* Linn. f. in New Zealand by Wardle (1966) and Stewart (1986) and of *W. trichosperma* Cav. in Chile by Veblen *et al.* (1981) indicate that the regeneration of these species is largely dependent on the presence of large openings in the forest canopy such as are caused by earthquake triggered landslides, volcanic eruptions and floods. In fact, Veblen *et al.* (1981) describe *W. trichosperma* as a "shade intolerant, extreme opportunist species". Observations in montane regions of New Guinea and Vanuatu suggest that other species have similar ecological requirements. Also it is well known that the Andes, where the majority of *Weinmannia* species occur, is a region of great tectonic activity. In contrast, Australia is currently geologically quiescent, and lacks mountainous topography with areas prone to large-scale disturbance. Probably this has also been so for long periods during the Tertiary and may have been a significant factor in the extinction of this genus from Australia, as Hill (1990a) has summarised for some species of *Nothofagus* and several gymnosperms. Floyd (1981) also notes that *C. serratifolia* and *Schizomeria ovata* are typical pioneer species in disturbed rainforests and in

adjoining sclerophyll forest.

An element of the Cethana flora which probably occurred in topographically highly shaded niches is represented by at least two deciduous *Nothofagus* species, *Pterostoma* aff. *anastomosans* and various evergreen conifers. This can be related to the high southern latitude at the time of deposition, and there is various support in the literature for such conclusions. During the long winters broad-leaved evergreen plants receiving little or no illumination would experience a net photosynthetic/respiratory imbalance, particularly if temperatures remained relatively warm. Read and Hill (1985) and Read (1990) found that the winter deciduous Tasmanian alpine/sub-alpine endemic *Nothofagus gunnii* is difficult to cultivate in lowland Tasmania and Read (1990) suggested that this may be due to high dark respiratory losses during mild summer nights. The presence of *Ginkgo* leaves in probable Eocene sediments in Tasmania as well as relatively large-leaved deciduous *Nothofagus* is support for this concept (Hill and Carpenter unpublished). Bond (1989) convincingly argues that gymnosperms will be restricted to areas where growth of angiosperm competitors is reduced, especially by cold and nutrient and light shortages.

Ferns closely comparable to the Cethana macrofossils now occupy a broad diversity of habits, from epiphytic (e.g. Hymenophyllaceae), to climbing (*Lygodium*), ground-dwelling (e.g. *Blechnum*, *Sticherus*, *Gleichenia*) and arboreal (Cyatheaceae). Spores assignable to the extant tree fern taxa Cyatheaceae, *Lophosoria* and *Dicksonia* also occur. Biogeographically, associations of all of the modern affinities of the macrofossil taxa may be found in eastern Australia, New Zealand, Malesia and the Pacific. Page and Clifford (1981) have already noted that the fern floras of these Gondwanic regions and South America and South Africa show strong taxonomic links. Ecologically, this element is predominant in montane regions of the tropics, and also occurs at lower altitudes as latitude increases. The presence of the climbing fern *Lygodium* may be interpreted as being incongruous to this conclusion, as it is typically found in the lowland tropics. However, as it is exclusively a fern of well-lit situations, it may have occurred upwards beyond its

normal altitudinal limit along the open regions provided by water courses. I have observed this in Vanuatu. It may be that a similar situation also exists in regions where *Nothofagus* /podocarp dominated forest occurs in low to mid latitude regions such as New Caledonia and the North Island of New Zealand. Similarly, it should be acknowledged that typical high altitude light requiring taxa such as *Gleichenia* and *Sticherus* may descend below their usual altitudinal zones in tropical regions along rocky drainage lines if cool and moist microclimates are present. *Gleichenia* and *Schizaea* are ferns of open oligotrophic habitats such as could have occurred proximal to the lake.

In conclusion, the Cethana environment can be seen as a mosaic of communities growing in close proximity to a lake. It was similar in terms of climatic and edaphic factors to modern regions of Australasia today, but differed markedly in its high number of available light niches because of the extreme local relief and high latitude at the time of deposition. This combination of environmental conditions resulted in an extremely diverse local vegetation. Although the effects of fire are often interrelated, differences of community types according to aspect and steep topography and in close proximity to depositional sites are readily observable in Australia today, and frequently they contain floristic similarity to the Cethana fossil flora. In Tasmania, an island of rugged topography where the yearly variation in photoperiod is obviously the greatest of any area in Australia, basically nanophyllous open scleromorphic communities containing *Allocasuarina*, Leguminosae and Epacridaceae can be observed on the north-facing slope of a river while mesic wet sclerophyll forests including cool temperate rainforest taxa occur on the south facing slope. Often, litter from both communities can be observed in the water. Along the Great Dividing Range of eastern Australia there is juxtaposition of rainforest and sclerophyllous vegetation. For example, at the escarpment at Point Lookout in New South Wales, sclerophyllous shrubs and trees such as *Lomatia fraseri* and *Banksia spinulosa* occur on the dry ridgelines, with temperate rainforest containing *Nothofagus moorei*, *Elaeocarpus holopetalus*, *Vesselowskya moorei*, *Callicoma serratifolia* and *Ceratopetalum apetalum* on sheltered slopes below. Waterside

environments themselves usually represent ecotones with significantly different humidity, radiation incidence and edaphic factors compared to that experienced inside the forest proper.

As discussed in Chapter 2.1 the topography, elevation and soils in the Cethana region today are probably not unlike those which occurred in the Early Tertiary near the fossil site. The vegetation on the Moina sandstone is highly sclerophyllous and dominated by small trees of *Eucalyptus nitida* Hook. f. and *Acacia mucronata* Willd. ex H. Wendl. and xeromorphic shrubs such as *Leptospermum* species (Myrtaceae), Epacridaceae, other legumes, *Banksia marginata* Cav. and *Lomatia tinctoria.* It is interesting to speculate that sclerophyllous plants have been selected for in the region since at least the Early Tertiary.

CHAPTER 7

COMPARISON WITH OTHER FLORAS

Although many macrofossils remain to be identified, the relatively high number of taxonomic determinations from the Cethana deposit established in this thesis enables meaningful comparison with other Australian deposits of similar age. These include the Vegetable Creek flora from the New England Tableland of New South Wales which was described by Ettingshausen (1888). He attributed all the fossils from the region to a single flora, but the assemblage is actually a composite of several differently aged sites (Pickett *et al.* 1990). Hill (1988a) examined organically preserved macrofossils and confirmed the presence of Lauraceae and *Nothofagus* leaves with close affinity to *N. moorei* and the fossil species *N.tasmanica.* These fossils were from Witherden's Tunnel which has been dated palynologically as Late Eocene (Hill 1988a). A study of fossils named by Ettingshausen from another Vegetable Creek site, the Old Rose Valley Lead has revealed some important comparisons to the Cethana flora. Pickett *et al.* (1990) reassessed the age of these sediments as younger than 30.4 $\pm$ 0.3 Ma (Late Oligocene) based on their probable correlation to nearby basalts. None of these fossils has organic preservation and they have not been critically re-examined. However, Ettingshausen's descriptions and illustrations are generally of high quality, and taxonomic interpretations of some of them can be made with confidence. There are some notable similarities to taxa identified from Cethana. Of particular interest is the co-occurence of the cycad-like plant Ettingshausen named *Anomozamites muelleri*, but there are probably also two ferns and numerous conifers and angiosperms in common, at least at the generic level. These are (with Ettingshausen's determinations in brackets); probably Cyatheaceae (*Pteris torresii*), *Lygodium* (*L. strzeleckii*), *Libocedrus* and possibly imbricate *Dacrycarpus*, *Lagarostrobos* or *Dacrydium* (*Heterocladiscos thujoides*), *Phyllocladus* (*P. asplenioides*), *Agathis* (*Dammara intermedia, D. podozamioides*), possibly *Podocarpus* (*Sequoia australiensis*), *Gymnostoma* (*Casuarina cookii*), *Nothofagus muelleri* (Ett.) Paterson (*Fagus celastrifolia, Fagus hookeri*- see Hill 1988a), Lauraceae (e.g. *Ficus gidleyi*), *Banksieaeformis* similar to *Dryandra formosa*

(*D. prae-formosa, D. benthami*), probably *Lomatia* (*Rhopala sapindifolia*), other Proteaceae (e.g. *Sassafras lesquereuxii*), *Brachychiton* (*Aralia prisca, A. oxleyi*) and microphyllous Myrtaceae (e.g. *Callistemophyllum beckeri*). None of the other taxa recognised by Ettingshausen are definitely absent from Cethana, so it can be concluded that this Vegetable Creek flora is floristically very similar to Cethana. Further, on the available evidence these floras are more similar to each other than either is to the geographically intermediate lowland Eocene floras discussed by Christophel and Greenwood (1989). It is also notable that the mean leaf length of specimens from the Vegetable Creek site is similar to that of Cethana (Fig. 5.1). This evidence strongly suggests a microthermal flora and it seems that it was actually in place on the New England tableland by the Late Eocene (Hill 1988a). In fact, Feary *et al.* (manuscript submitted) consider that when coldest Cainozoic sea surface temperatures occurred in the Oligocene, the entire north-eastern Australian region was within the temperate zone. There is evidence that associated with the polar ice build -up the sea level fell, so that at Vegetable Creek (now 650 m a.s.l.) the climate would have been quite cool. I consider it likely that these conditions enabled *Nothofagus* and numerous other microthermal elements to reach New Guinea around this time and the Great Dividing Range can be envisaged as a portal. This is consistent with pollen records from sites in eastern Australia and New Guinea through the Tertiary as summarised by Martin (1982). If, as seems likely, the Old Rose Valley Lead is more recent than Cethana then the reason for the apparent similarity of their floras probably lies in the marked cooling which occurred around the time of deposition and the effects of altitude at Vegetable Creek.

The floristic, physiognomic and aspects of ecological similarity of the Late Oligo-Miocene Yallourn and Morwell coals described in detail by Blackburn (1985) to Cethana has already been referred to. This flora is more recent than Cethana. It is most notable that it also contains a very high diversity of *Banksieaephyllum* and several other sclerophyllous and sometimes xeromorphic macrofossil taxa including *Gleichenia*, aff. Restionaceae, Casuarinaceae, Epacridaceae and *Baeckea* (Myrtaceae). Also present are the podocarps *Dacrydium rhomboideum*, *Phyllocladus*

morwellensis, *Dacrycarpus morwellensis* (Hill and Carpenter 1991-appendix I) and aff. *Microcachrys*, *Araucaria ligniticii*, *Agathis yallournensis*, as well as leaves or fruits from more typical rainforest taxa including *Gymnostoma*, *Quintinia*, *Elaeocarpus*, Araliaceae, Myrtaceae and Proteaceae. Although *Nothofagus* pollen is common (Luly *et al.* 1980) macrofossils are lacking. Blackburn was able to show a positive relationship between the most xeromorphic of these taxa and edaphic factors (especially periodic water stress) and the presence of fires. He, and Luly *et al.* (1980) have also stressed that there were admixtures of plants which today grow in widely different environments. They envisaged a swamp vegetation within the basin of accumulation composed largely of conifers and several monocots and sclerophyllous angiosperms. In the surrounding catchment areas rainforests of cool temperate and subtropical affinity occurred. At Cethana these communities apparently grew much closer to the depositional site.

In Tasmania Cethana is probably slightly more recent than the Late Eocene Loch Aber deposit and older than the relatively well studied Oligocene Pioneer and Little Rapid River deposits (Hill and Macphail 1983; Hill 1990). Each of these also contains abundant (and at Little Rapid River diverse) *Nothofagus* macrofossils and Cupressaceae, Araucariaceae and numerous genera of Podocarpaceae. Other angiosperms are generally less common but include Lauraceae, Cunoniaceae, Escalloniaceae, Myrtaceae, *Eucryphia*, occasional Proteaceae and *Gymnostoma*. Only one species of *Banksieaephyllum* occurs in each of the Pioneer and Loch Aber deposits. This genus is lacking from Little Rapid River but this deposit contains microphylls of Epacridaceae.

There are several Middle Eocene deposits in south-eastern mainland Australia, of which the best known are Nerriga (Hill 1982, 1986) and Anglesea (Christophel and Greenwood 1987, 1989; Christophel *et al.* 1987). Nerriga features diverse and abundant Lauraceae (Hill 1986) and was probably deposited under mesothermal conditions (Christophel and Greenwood 1989; Hill and Carpenter unpublished). The situation at Anglesea is less clear because the deposit is composed of discrete lenses (Christophel *et al.* 1987) which have very different physiognomic characters (Fig.

5.1). Christophel refers to a complement of taxa recognised in each of three floras as "key" components of the Tertiary vegetation. He makes much of what he considers to be a floristic and physiognomic similarity of Anglesea to the Noah Creek region of north-eastern Queensland. However, 100 + macrofossil taxa occur at Anglesea, and only about 10% of them have been positively identified to generic level (*Gymnostoma*, *Pterostoma*, *Austrodiospyros*, *Banksieaephyllum*, *Brachychiton*, *Myrtaciphyllum*, *Quintinia*, *Podocarpus*, *Retrophyllum*, *Dacrycarpus*, *Prumnopitys* and *Falcatifolium*; Christophel *et al.* 1987; Greenwood 1987). As discussed, many of these relatively easily identifiable taxa also occur at Cethana, indicating that they were indeed quite temporally and spatially widespread. This fact, the absence of some of these genera from Australia, and the fact that only about 10% of the total Anglesea macroflora has been identified indicates that caution should be adopted in nominating perceived small regions of extant vegetation as models for entire fossil floras. This also stresses the importance of detailed floristic analyses.

CHAPTER 8

CONCLUSION

Study of the Cethana flora to date supports the existing understanding of the nature of Early Tertiary floras in south-eastern Australia and particularly in Tasmania. In addition, because of the floristic emphasis of this study, much novel information has been produced. For instance;

1) a diverse, highly sclerophyllous element existed in the vegetation well before the onset of widespread aridity in the region. The Proteaceae was an important component of this flora, and included taxa with pronounced gross morphological similarity to species of *Banksia* and *Dryandra* now confined to Western Australia.

2) previous study on south-eastern Australian Tertiary macrofloras had established that taxa which have nearest living relatives in regions such as Tasmania, Queensland, New Zealand, New Caledonia and New Guinea once co-occurred. However, in general, despite their geographic separation these taxa occupy similar rainforest environments. This study of the Cethana flora demonstrates that taxa with nearest living relatives which have diverse ecological requirements also grew in close proximity, albeit in a range of quite different habitats. The co-occurrence of taxa with nearest living relatives now distributed widely geographically and ecologically is testament to the existence of environments in the Early Tertiary which have no modern equivalent but also demonstrates that these environments were able to support highly diverse floras. There is no doubt that the Oligocene rainforests of Tasmania were much more diverse than at present.

3) the identification of *Callicoma serratifolia* and *Vesselowskya* aff. *rubifolia* in a flora containing abundant *Nothofagus tasmanica* is highly significant, since it provides strong support for the hypothesis that *N. tasmanica* is very closely allied to *N. moorei* (Hill 1983b). *C. serratifolia*, *V. rubifolia* and *N. moorei* are now associated in the rainforests of north-eastern New South Wales, and apparently survive in a climate very similar to that which occurred in Tasmania in the Oligocene.

4) extinct gymnosperms, presumably at least at the family level, were still present in the southern floras in the Oligocene. At least some of them may have been

deciduous taxa which were able to maintain their competitiveness at high latitudes in shaded habitats.

5) the Cethana flora is the first Tertiary macrofossil flora studied to show a significant pteridophyte component.

A number of future research directions are suggested which relate not merely to 'palaeobotany' but to botanical research in general. Direct further study on the Cethana site is advocated. In particular a thorough taphonomic and sedimentary study of the depositional site may enable distinct communities in the flora to be identified with greater confidence. Also, as suggested, the diversity of the flora can be expected to increase markedly with further collection and recovery of specimens. This could be achieved most rapidly by dispersed cuticle preparation and analysis.

The fossil record offers concrete data for biogeographical interptetations of extant floras. Also of special interest are the questions it raises relating to the physiological tolerances of plants and their growth under climatic conditions not experienced today and at southern latitudes where woody plants no longer grow.

The increasing evidence that the Oligocene floras of Tasmania and elsewhere contain a distinct taxonomic and physiognomic similarity to rainforests now confined to upland regions of eastern Australia and New Guinea in particular suggests that these should be regarded as 'target' areas for enabling identification of further fossil taxa. It is not a particularly difficult task to gather and store leaves and cuticles of all these taxa for comparative study. The species with non-entire leaves are an obvious starting point.

Considering the abundant and taxonomically rich complement of proteaceous fossils at Cethana and elsewhere in the Tertiary, and the importance of this family to the Australasian flora, a comprehensive study of Proteaceae cuticles is proposed in order to facilitate macrofossil identification. Also, this family is ideal for exploring the relationships between the degree of cuticular xeromorphy and climatic and edaphic influences. The identification of numerous Cunoniaceae macrofossils indicates that this family should be the subject of further systematic and ecological research. A bioclimatic assesssment of *Callicoma* and *Vesselowskya* could be

undertaken to add to climatic understanding of the Cethana environment. Studies are also under way using fossil germlings to study past climates.

The potential of studying the DNA from well preserved fossils has been established by Golenberg *et al.* (1990) who extracted and amplified a segment from the chloroplasts of Miocene *Magnolia* leaves from North America. This technique could be applied to mummified leaves from several Australian Tertiary floras in order to add to existing interpretations of their taxonomy and relationships.

This study emphasises the importance of palaeobotanical study for understanding the development of the modern Australian flora. It reminds us that despite the apparent antiquity of certain taxa and uniformitarian physiological/physiognomic restraints, the plant associations we see today are in a state of flux, with a constant sifting and migration of taxa.

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APPENDIX I

PAPERS IN PRESS

Carpenter, R. J. (1991). *Macrozamia* from the Early Tertiary of Tasmania and a study of the cuticles of extant species. *Australian Systematic Botany* **4**.

Hill, R. S. & Carpenter, R. J. (1991). Evolution of *Acmopyle* and *Dacrycarpus* (Podocarpaceae) foliage as inferred from macrofossils in south-eastern Australia. *Australian Systematic Botany* **4**.

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Macrozamia from the Early Tertiary of Tasmania and a Study of the Cuticles of Extant species

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Abstract

A new species of *Macrozamia, M. australis*, is described from the Oligocene Cethana deposit. Cuticular characters can be used to separate the two sections of the genus but the combination of cuticular features of *M. australis* is unique. Analysis of extant adult and juvenile cuticles confirms that section *Parazamia* is composed of neotenous species but indicates that this may not be a monophyletic group. The ecological significance of the presence of *Macrozamia* in a macrofossil flora which contains numerous microthermal rainforest elements (including *Nothofagus*) and sclerophyllous taxa is discussed.

Introduction

Of the 10 living cycad genera four are found in a narrow zone on the east coast of Australia, in New South Wales and Queensland. These are *Cycas* (Cycadaceae) and the endemic *Lepidozamia, Bowenia* and *Macrozamia* (Zamiaceae). *Lepidozamia* and *Bowenia* have also been described from Eocene and Oligocene deposits in Victoria and New South Wales (Cookson 1953; Hill 1978, 1980). The cuticle of the fossil *L. hopeites* (Cookson) L. Johnson is almost identical to that of extant *L. hopei* (Johnson 1959). The two extant *Bowenia* species and *L. hopei* are restricted to small regions of north-eastern Queensland near or within rainforest.

The only other confirmed record of Australian Tertiary cycads with organic preservation is that of Hill (1980) who described two species of an extinct genus, *Pterostoma*, from Eocene deposits of south-eastern Australia. *Pterostoma* has since been recovered from Cethana and the Eocene Buckland deposit in Tasmania. It also occurs in the Miocene Yallourn clays (D. R. Greenwood, personal communication). Pant (1987) reassigned the *Pterostoma* species described by Hill (1980) to *Macrozamia* on the basis of the presence of sinuous cell walls and what he believed to be a similarity of frond architecture. This proposal is rejected since *Pterostoma* has many distinctive features which never occur in *Macrozamia*. These include the presence of frequently dichotomosing and anastomosing veins, random stomatal orientation, and pronounced cuticular surface ornamentation. In addition, the base of the rachis in *Pterostoma* is enlarged, giving the appearance of an abscission zone (Hill 1980).

Macrozamia is the largest and most widely distributed cycad genus in Australia. In his review of the Zamiaceae, Johnson (1959) recognised 14 species of *Macrozamia* of which 11 occur in New South Wales and 5 in Queensland. These are absent from the tropical rainforest regions of north-eastern Queensland. Instead they are mostly restricted to nutritionally poor,

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frequently siliceous soils in *Eucalyptus* dominated sclerophyll communities south of the Tropic of Capricorn (Johnson 1959). Two other closely related *Macrozamia* species have disjunct distributions between central and western Australia. *Macrozamia riedlei* is associated with the diverse sclerophyll flora of south-western Western Australia and *M. macdonnellii* is found only in and around the arid Macdonnell Ranges of the Northern Territory. Its relict status is especially evident at Palm Valley because it is sometimes associated with *Livistona mariae* palms, which occur nowhere else.

Two sections of *Macrozamia* are recognised by Johnson (1959, 1961). Mature plants of section *Macrozamia* are generally large and arborescent and their pinnae have mucilage canals and lack prominently raised veins on their lower surfaces. Species are found in western, central and eastern Australia. Johnson (1959) considered section *Macrozamia* to be the more primitive or conservative since the species of the other group, section *Parazamia*, show evidence of reduction and neoteny. For instance, the adult pinnae of species in section *Parazamia* are difficult to distinguish from those of juveniles in section *Macrozamia*. Section *Parazamia* is restricted to eastern Australia and the ranges of species sometimes overlap those of section *Macrozamia*. Johnson (1959, 1961, 1963) records a few apparent hybrids, recognised by their obviously intermediate frond characters and their occurrence as rare individuals in mixed communities of the parents, but states that the specific limits do not break down.

In the present study a fossil *Macrozamia* species is described and the cuticular features of modern species investigated in an attempt to determine its affinities. The significance of the discovery of *Macrozamia* in a deposit that is considered to have been laid down under cool and mesic conditions is discussed, along with the implications of the cuticular analysis of the genus.

Location and Age of the Deposit

The deposit is located near the Cethana Dam, northern Tasmania (41° 32' S., 146° 07' E.). Determination of geological age is based solely on fossil stratigraphy since the sediments unconformably overlie Ordovician sandstone (Hill 1984). Palynological investigations indicate that the deposit is of Oligocene age (Hill and Carpenter, unpublished data) and by comparison to the taxonomic and physiognomic composition of numerous other Tasmanian macrofossil assemblages is likely to be early Oligocene. Conifer macrofossil remains include a diversity of Araucariaceae, Podocarpaceae and *Papuacedrus* (Cupressaceae). Numerous *Nothofagus*, Proteaceae and Cunoniaceae species have also been identified as well as several ferns (Hill 1984; Carpenter 1988; Carpenter and Hill 1988; Hill and Christophel 1988; Hill and Carpenter, unpublished data).

Materials and Methods

The type specimen was photographed with an Olympus OM2 35-mm camera using reflected light. Small fragments of organic material remain on this fossil. Pieces were placed in hydrofluoric acid (HF) to dissolve adhering siliceous matter and then treated with cold 10% chromium trioxide until the cuticle separated from the mesophyll. Cuticle fragments were then rinsed in water and 10% aqueous ammonia and either stained with 1% safranin and mounted in phenol glycerin jelly for light microscopy or placed on aluminium stubs with double-sided adhesive tape for scanning electron microscopy. The stubs were then sputter coated with gold to a maximum thickness of 20 nm and examined using a Philips 505 SEM operated at 15 kV.

Pieces of sediment from different horizons to that in which the type specimen was found were placed in a 200 mL beaker and disaggregated by agitation in a solution of neutral detergent and hot water for at least 48 h. The resultant slurry was then sieved and trapped fragments of organic material were rinsed into a 100 mL plastic beaker. The water was decanted and replaced with HF. The procedure outlined above was then followed to prepare dispersed cuticle slides. Over 20 such slides were prepared.

Adult pinnae from all extant *Macrozamia* species except *M. lucida*, as well as pinnae from several juveniles and putative hybrids were obtained from the National Herbarium of New South Wales or the Department of Plant Science, University of Tasmania (Table 1). Segments from the median region of each were treated in the same manner as the fossils, or first heated in hydrogen peroxide until cleared. This method was used for those species in which cuticle did not separate from the mesophyll within 48 h.

Cuticular features of the fossil and extant specimens were compared using light and scanning electron microscopy. *Macrozamia* taxonomy follows the revisions of Johnson (1959, 1961).

Table 1. Herbarium specimens examined
Unless otherwise denoted all specimens were obtained from the N.S.W. Herbarium

Taxon	Collector's name and number	Collection date	Collection locality and herbarium no. (if no N.S.W. collector's no.)
M. macdonnellii (F. Muell. ex Miq.) A.DC.	*R. A. Perry 3498*	21.iii.1953	Palm Valley, N.T.
M. miquelii (F. Muell.) A.DC.	*W. McReaddie*	29.ix.1966	Goodnight Scrub, Mt Perry Range (83914), Qld
M. miquelii (F. Muell.) A.DC. juvenile	*J. L. Boorman*	Aug. 1912	Mt Perry, Qld
M. riedlei (Fisch. ex Gaudich.) C. A. Gardn.	*P. J. Lang 1365, Adel. Uni.*	23.ix.1978	Howick Hill, *c.* 90 km E. of Esperance (Plant Sci. Tas. Uni. E/M/027), W.A.
M. riedlei (Fisch. ex Gaudich.) C. A. Gardn. juvenile	*L. Haegi 1814*	15.vii.1979	Walpole-Nornalup N.P., W.A.
M. moorei F. Muell.	*J. L. Boorman*	Jan. 1907	Dalmorton (40966), N.S.W.
M. moorei F. Muell. juvenile	*L. A. S. Johnson LJ 8602*	27.iv.1981	15 km N. of Mt Moffat homestead, Qld
M. moorei F. Muell. semi-juvenile	*W. Morris*	Jan. 1960	3 miles E. of Dalmorton (49024), N.S.W.
M. communis L. Johnson	*R. S. Hill. Tas. Uni.*	Mar. 1988	southern N.S.W. (Plant Science, Tas. Uni. E/M/009)
M. communis L. Johnson not mature	*H. Salasoo 1347*	13.iii.1955	Nowra to Cabbage Tree Creek, N.S.W.
M. communis L. Johnson juvenile	*R. Ornduff 9585*	23.i.1987	Smith's Lake along Ski Cove Rd, E. of Bulahdelah, N.S.W.
M. diplomera (F. Muell.) L. Johnson	*L. A. S. Johnson*	2.iv.1961	4 miles S. of Bugaldi, towards Yearinan (53845), N.S.W.
M. diplomera (F. Muell.) L. Johnson	*R. Ornduff 9565*	16.i.1987	Guinema rd junction with Coonabarabran-Baradine rd, N.S.W.
M. heteromera C. Moore	*R. Ornduff 9572C*	17.i.1987	5·5 km along Dandry rd, N. of Oxley Hwy, nr Coonabarabran, N.S.W.
M. heteromera C. Moore	*R. Ornduff 9567*	16.i.1987	0·4 km along E. side of Dandry rd, nr Coonabarabran, N.S.W.
M. heteromera C. Moore	*R. Ornduff 9569A*	Jan. 1987	lookout path near E. entrance, Warrumbungle N.P., N.S.W.
M. heteromera C. Moore	*E. F. Constable 44*	12.xii.1961	'Guneemooroo' *c.* 8 miles NE. of Tooraweenah, N.S.W.
M. heteromera C. Moore	*W. Morris*	Jan. 1960	halfway from Narrabri to Coonabarabran (49025), N.S.W.
M. stenomera L. Johnson	*J. R. Hosking*	24.vii.1985	Oxley Park, Tamworth, N.S.W.

R. J. Carpenter

Taxon	Collector's name and number	Collection date	Collection locality and herbarium no. (if no N.S.W. collector's no.)
M. stenomera L. Johnson	*A. Rodd 3331 & A. Blombery*	8.iii.1978	Coryah Gap, Mt Kaputar N.P., N.S.W.
M. stenomera L. Johnson	*A. Rodd 3331*	8.iii.1978	Coryah Gap, Mt. Kaputar N.P., N.S.W.
M. platyrachis F. M. Bail.	*D. F. Blaxell 860*	27.xi.1972	Mimosa Ck, nr Forestry Camp, Blackdown Tableland, Qld
M. secunda C. Moore	*K. Hill 2780* et al.	21.x.1987	Gungal rd, 16·5 km from Merriwa, N.S.W.
M. spiralis (Salisb.) Miq.	*P. Hind 5447*	18.xi.1987	fire-trail off Spence rd, opp. Judd st., Berkshire Pk, Sydney, N.S.W.
M. spiralis (Salisb.) Miq. juvenile	*R. Harrison*	May 1955	Wallacia district, N.S.W.
M. fawcettii C. Moore	*E. F. Constable 1339*	19.x.1961	Halfway Ck, Barcoongere SF, 20 miles SE. of Grafton, N.S.W.
M. fawcettii C. Moore juvenile	*D. Blaxell*	13.xi.1958	about 15 miles S. of Tabulam (46188), N.S.W.
M. pauli-guilielmi W. Hill *et* F. Muell.			
M. pauli-guilielmi ssp. *pauli-guilielmi*	*L. A. S. Johnson*	Apr. 1958	cultivated Royal Botanic Gardens (43384), N.S.W.
M. pauli-guilielmi ssp. *plurinervia* L. Johnson	*K. Hill 2787A & L. Stanberg*	4.v.1988	Camerons Gorge Nature Reserve, N.S.W.
M. pauli-guilielmi ssp. *flexuosa* (C. Moore). L. Johnson	*H. Salasoo 3370*	7.i.1967	N. shore of Smith Lake, S. of Forster, N.S.W.
M. moorei x *M. lucida*	*L. A. S. Johnson & E. F. Constable*	7.vi.1957	3 miles E. of Dalmorton (43070), N.S.W.
M. communis x *M. pauli-guilielmi* ssp. *flexuosa*	*W. Morris*	Oct. 1959	Kahibah (47612), N.S.W.
M. diplomera x *M. heteromera*	*J. L. Boorman*	Jun. 1915	cultivated Sydney Botanic Gardens (40633), N.S.W.

Taxonomic Description

Order Cycadales
Family Zamiaceae

Macrozamia Miq. (1842)

Macrozamia australis R. J. Carpenter, sp. nov. (Figs 1–8)

Diagnosis

Pinna hypostomatic. Stomates in loose rows restricted to areas between veins and oriented parallel to veins. Stomates in pits usually surrounded by five or six subsidiary cells. Normal epidermal cells on upper surface and venous cells on both surfaces arranged in long parallel files, usually rectangular or with oblique end walls, periclinal walls of variable thickness. Epidermal and subsidiary cells within stomatal rows usually shorter. Trichome bases abundant along the margins. Crystalliferous cells less frequent along the margins and on lower surface veins.

Description

Architecture. The holotype (specimen C-532) is a pinna fragment 1·9 cm long and 0·6 cm wide (Fig. 1). The impressions of 12 or possible 13 non-branching and non-anastomosing veins are visible. Since the fragment does not taper to either end and the veins are parallel it is assumed that it came from near the centre of the pinna.

Abaxial epidermis. Stomates occur in widely separated rows (3–10 epidermal cells) between the veins which are about 15 epidermal cells wide (Fig. 2). Stomatal width averages 35·5 μm (33·0–40·0 μm) and average length of stomatal aperture is 27·0 μm (24·0–32·0 μm). Guard cell polar extensions were rarely preserved and the length of stomates with preserved polar extensions is about 48 μm. The sunken guard cells are overarched by 4–7 (average 5·4) subsidiary cells per stomate (Figs 2–4) which form a mound slightly raised above the cuticular surface (Fig. 5). The end walls of the subsidiary cells facing the pit are usually convex and substantially thickened. Epidermal cells are arranged in longitudinal rows, joined end-to-end by transverse, oblique or tapering end walls (Figs 2 and 6). Anticlinal walls are not buttressed or sinuous. Epidermal cell length averages 86·5 μm (35·0–190·0 μm) and width 15·5 μm (12·5–21·0 μm). The average L:W ratio of these cells is 4·6. The periclinal walls of the epidermal cells stain differently as they are of variable thickness (Fig. 2). The surface view outlines of the epidermal cells are distinct, particularly along the veins (Fig. 6). Trichome bases (Fig. 7) and a few crystalliferous cells (Fig. 8) occur along the pinnae margins. The latter also occur, but less frequently, along veins between the stomates.

Adaxial epidermis. Stomates absent. Epidermal cells of similar size and arrangement to those on the abaxial surface. Trichome bases abundant along the margin.

Holotype. Specimen number C-532 and counterpart, housed in the Department of Plant Science, University of Tasmania.

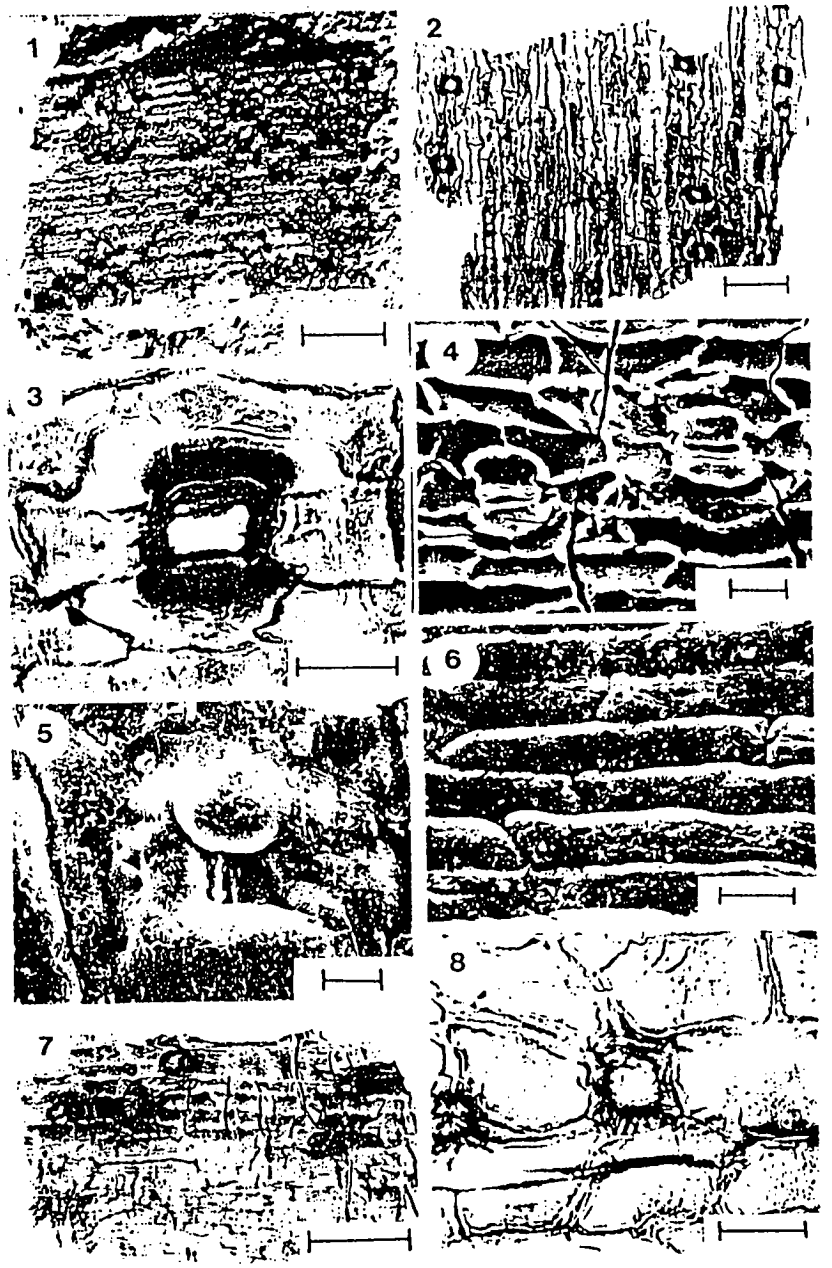
Type locality. Cethana, Tasmania (41° 32' S., 146° 07' E.).

Etymology. Named for the extreme southerly record of *Macrozamia.*

Specimens examined. C-532, and dispersed cuticle fragments C-651, 652.

Comparison of Fossil and Extant Species

The fossil species has features which match those of *Macrozamia* and *Lepidozamia* according to the keys and descriptions of Greguss (1968). However, the two genera are readily separable, since in *Lepidozamia* the long axes of the epidermal cells are oblique or transverse to the long axis of the pinna whereas those of *Macrozamia* are parallel (Cookson 1953; Johnson 1959; Hill 1980). The epidermal cells of the fossil are clearly aligned parallel to the long axis of the pinna (Fig. 2) and the specimen is therefore assigned to *Macrozamia* with confidence. Pant and Nautiyal (1963) and Greguss (1968) examined cuticles of seven and eight species of *Macrozamia* respectively using light microscopy. No attempt was made to identify features which could be used to segregate the two sections. Instead the species were sorted into groups using features such as the distribution of stomata (hypostomatic or amphistomatic), length to width ratios of epidermal cells, the nature of the anticlinal walls (straight or sinuous), the degree of sunkenness of the guard cells and the presence of crystalliferous cells. Many of these characters appear to be taxonomically significant, but since not all species were examined



Figs 1–8. *Macrozamia australis.* **Fig. 1.** Portion of specimen C-532 showing organic fragments and veins. Scale: 2 mm. **Fig. 2.** Abaxial cuticular surface showing distribution of stomata, a vein and unevenly staining epidermal cells. Scale: 100 μm. **Fig. 3.** Stomate, with four subsidiary cells. The guard cells are sunken well below the level of the epidermis. Scale: 25 μm. **Fig. 4.** SEM of inner cuticular surface showing stomata with pronounced guard cell cuticular flanges. Scale: 25 μm. **Fig. 5.** SEM of outer cuticular surface with a stomatal pit. Note the raised mound and the polar subsidiary cell with convex end wall thickening. Scale: 10 μm. **Fig. 6.** SEM of outer cuticular surface showing clearly defined venous epidermal cell outlines with transverse and oblique end walls. Scale: 25 μm. **Fig. 7.** Marginal cuticular surface showing several thickened trichome bases. Scale: 100 μm. **Fig. 8.** Crystalliferous cell. Scale: 10 μm.

and some seem to have been incorrectly identified, the usefulness of this data is limited. For the current study, cuticles of all extant species of adult *Macrozamia* as recognised by Johnson (1959, 1961) were compared using light and scanning electron microscopy. The results of this analysis are presented in Table 2. The following characters can be used to segregate the species into two groups, which conform to the two sections of the genus:

(1) The average number of subsidiary cells is higher than 6·5 for all species in section *Macrozamia* (Fig. 9) and less than 6·1 for all species in section *Parazamia* (Figs 10 and 11).

(2) Crystalliferous cells are found only in section *Macrozamia* where they are most abundant on the abaxial surface, particularly along the margins and adjavent veins (Fig. 12). These were recognised by Pant and Nautiyal (1963) but their origin and function are unknown.

(3) Sinuous or buttress walled epidermal cells are found only in section *Macrozamia* (Fig. 13). They are most noticeable on the adaxial surface.

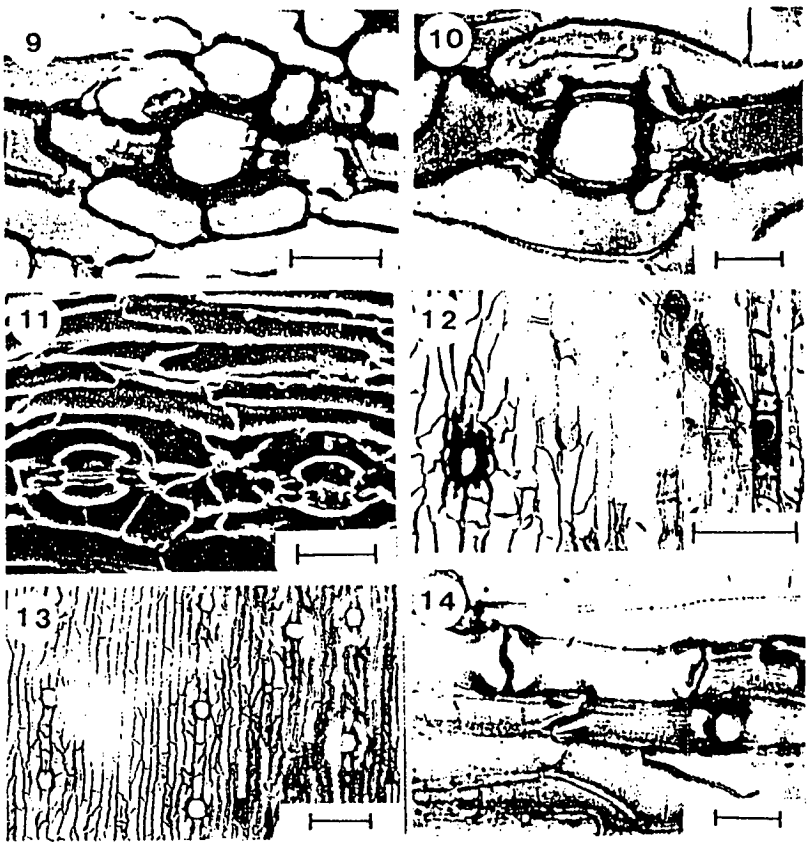
(4) The L:W ratio of the abaxial venous epidermal cells, although variable within a species, is usually much higher for species in section *Parazamia*. The abaxial surface was chosen because all species have stomates on this surface; however, adaxial venous cells appear to be similar.

Table 2. Cuticular characters of adult (A) and (J), putative hybrid and fossil *Macrozamia* specimens
Subsidiary cell number and length to width ratio of epidermal cells are average values of at least 50 stomatal and abaxial venous cells respectively per specimen. +, character present; –, absent; x, specimen unavailable; a, amphistomatic; h, hypostomatic. *M. stenomera* data were based on *A. Rodd 3331*

Taxon	Stomatal distribution		Subsidiary cell number		L:W of epidermal cells		Crystalliferous cells		Buttressed or sinuous cells		End wall papillae	
	A	J	A	J	A	J	A	J	A	J	A	J
Section *Macrozamia*												
M. macdonnellii	a	x	7·1	x	3·1	x	+	x	+	x	–	x
M. miquelii	h	h	7·3	5·5	4·7	14·4	+	–	+	–	–	–
M. riedlei	a	h	7·0	5·4	4·2	12·8	+	–	+	–	–	–
M. moorei	a	a	6·6	5·6	4·0	14·7	+	–	+	–	–	–
M. communis	h	h	6·8	5·5	3·1	17·0	+	–	+	–	–	–
M. diplomera	a	x	7·4	x	3·5	x	+	x	+	x	+	x
Section *Parazamia*												
M. heteromera	a	x	5·8	x	5·3	x	–	x	–	x	+	x
M. stenomera	h	x	6·0	x	5·9	x	–	x	–	x	+	x
M. platyrachis	h	x	5·4	x	12·4	x	–	x	–	x	–	x
M. secunda	h	x	5·8	x	10·5	x	–	x	–	x	–	x
M. spiralis	h	h	5·9	5·4	12·3	10·4	–	–	–	–	–	–
M. fawcettii	h	h	5·7	5·5	16·8	12·6	–	–	–	–	–	–
M. pauli-guilielmi ssp *pauli-guilielmi*	h	x	5·4	x	14·3	x	–	x	–	x	–	x
M. pauli-guilielmi ssp *plurinervia*	h	x	5·8	x	11·5	x	–	x	–	x	–	x
M. pauli-guilielmi ssp *flexuosa*	h	x	6·0	x	9·1	x	–	x	–	x	–	x
M. moorei x *M. lucida*	a	x	5·6	x	11·5	x	–	x	–	x	–	x
M. communis x *M. pauli-guilielmi* ssp *flexuosa*	h	x	5·9	x	7·7	x	–	x	+	x	–	x
M. diplomera x *M. heteromera*	a	x	5·4	x	6·2	x	+	x	+	x	+	x
Fossil												
M. australis	h		5·4		4·6		+		–		–	

Cuticular characters were also assessed for the juvenile pinnae of *Macrozamia* (Table 2). The results support the observation of Johnson (1959, 1961) that section *Parazamia* may be neotenous since the cuticles of the juveniles of section *Macrozamia* species have characteristics typical of adults of section *Parazamia*. An exception is that both juvenile and adult pinnae of *M. moorei* are amphistomatic. Analysis of the cuticles of the geographically proximal group comprising *M. diplomera* (section *Macrozamia*), *M. stenomera* and *M. heteromera* (section *Parazamia*) provides evidence that these section *Parazamia* species may be linked to *M. diplomera* or its immediate ancestor through neotenic speciation. In particular, all three species have pronounced surface papillae which abut at the end walls of the cells (Fig. 14). These were occasionally observed in other species but never reached the same density or level of development. Furthermore, the closely related species pair, *M. stenomera* and *M. heteromera*, are the only species in section *Parazamia* with an epidermal cell L:W ratio more typical of section *Macrozamia*. Johnson (1959, 1961) also notes that this is a remarkable group since all three species have divided pinnae and *M. heteromera* is the only amphistomatic member of

section *Parazamia*. In addition, the amphistomatic *M. diplomera* and *M. heteromera* are partly sympatric while the very closely related pair *M. stenomera* and *M. heteromera* are allopatric. Johnson recognises the confusion caused by the similarity and range overlap of *M. heteromera* and *M. diplomera* but states that the former 'is as clearly a member of section *Parazamia* as *M. diplomera* is of section *Macrozamia*' (Johnson 1959) and that these species 'show extraordinary parallelism' (Johnson 1963). He proposed that plants with divided pinnae have some selective advantage in the region and that some introgressive gene flow may also have occurred between populations of the three species. However, an alternative possibility is that the



Figs 9–14. Extant *Macrozamia* species. **Fig. 9.** Stomate of section *Macrozamia* (*M. miquelii*), with seven subsidiary cells. Scale: 25 μm. **Fig. 10.** Stomate of section *Parazamia* (*M. platyrachis*), with four subsidiary cells. Scale: 25 μm. **Fig. 11.** SEM of inner cuticular surface of *M. secunda*. Note similarity to *M. australis*, Fig. 4. Scale: 50 μm. **Fig. 12.** Marginal cuticular surface of *M. moorei* showing trichome bases and crystalliferous cells. Scale: 100 μm. **Fig. 13.** Adaxial cuticular surface of *M. moorei* showing stomatal distribution and sinuous epidermal cell walls. Scale: 100 μm. **Fig. 14.** Epidermal cuticular surface of *M. heteromera* showing pronounced papillae which abut at the end walls. Scale: 25 μm.

similarity of these species could be attributable to a relatively close relationship through neotenic speciation. The effects of variation, hybridisation and gene flow should not be dismissed since cuticle from a specimen of *M. stenomera* from Oxley Park, Tamworth (*J. R. Hosking*) shows less development of papillae than other specimens of the group and a specimen from Coryah Gap, Mt Kaputar National Park (*A. Rodd 3331 and A. Blombery*) has a few stomata on the adaxial surface. The putative hybrid between *M. diplomera* and *M. heteromera* from the Warrumbungle Mountains possesses features of both parent species (Table 2).

In some cases, section *Parazamia* collections are probably just intermediate stages of section *Macrozamia* species (L. A. S. Johnson, personal communication). For instance, Johnson, A. G. Floyd and A. Rodd strongly suspect that non-coning *M. lucida* populations, particularly those in New South Wales, are not in fact *M. lucida* but are composed of juvenile plants from section *Macrozamia* which in some cases show retarded development due to unfavourable environmental conditions (L. A. S. Johnson, personal communication). Thus, the suspected hybrid between *M. moorei* and *M. lucida* from near Dalmorton, N.S.W. is probably an intermediate stage, a conclusion not contradicted by cuticular study (Table 2). However, the fact that the distributions of other section *Macrozamia* species do not overlap but populations of section *Parazamia* species are frequently intermingled with them (Johnson 1959) may indicate that other neotenic speciation events have occurred. Thus the situation is far from simple. To resolve this intriguing problem the life histories of plants from populations across the range of each species of *Macrozamia* would have to be examined and molecular taxonomic methods employed.

Analysis of the cuticle of *M. australis* demonstrates that this species cannot be assigned to either modern section (Table 2). It possesses the low average number of cells surrounding the stomatal pit characteristic of section *Parazamia*, and the presence of marginal crystalliferous cells and low L:W ratio of epidermal cells characteristic of section *Macrozamia*. Cell walls are not sinuous or buttressed. The presence of loose stomatal rows restricted to one surface is unique. These stomatal rows appear more like those of the adaxial surface of amphistomatic species such as *M. moorei* (Fig. 13). All extant hypostomatic species have much more closely packed stomates in distinct bands between the veins.

M. australis has 12 or possibly 13 veins. This is within the range of all species of section *Macrozamia* whereas only *M. fawcettii* of section *Parazamia* may have 10–13 veins (Johnson 1959). The stomatal pits of species in section *Parazamia* are quite shallow whereas those of most species in section *Macrozamia* are relatively deep. In section *Macrozamia* this is most pronounced in *M. macdonnellii* from arid Central Australia, and least pronounced in *M. miquelii* from the much more mesic Fraser Island. The degree of sunkenness of the stomates of the fossil is similar to that of species in section *Parazamia* and *M. miquelii.*

In the absence of reproductive and other vegetative evidence the phylogenetic status of *M. australis* must remain unclear, although it appears to have no close relationship to any extant species. The presence of dispersed cuticle of *M. australis* indicates that the fossil specimens were not from an intermediate ontogenetic stage of the plant. The combination of cuticular characters has not been observed in juvenile or hybrid pinnae either.

Discussion

The Cethana flora appears to be composed of elements from rainforest and non-rainforest communities growing in cool conditions of uniformly high rainfall and humidity. *Nothofagus* macrofossils are common and include taxa with close affinity to species now restricted to high latitude cool temperate rainforests of Tasmania and New Zealand (Hill 1984). A great diversity of conifer macrofossils have also been recovered, the bulk of which have affinity to living species in montane regions of the tropics (Hill and Carpenter, unpublished data). There is no extant vegetation type in which *Macrozamia* and microthermal rainforest elements are associated. However, according to Walker and Flenley (1979) *Macrozamia* pollen occurs in Late Quaternary sediments from the Papua New Guinea highlands, which are dominated by microthermal rainforest taxa. Unfortunately there are no other details concerning this interesting record.

A distinct element of the Cethana flora appears to be derived from an open sclerophyll community of boggy, rocky or sandy regions adjacent to the depositional site. Carpenter and Hill (1988) listed numerous such taxa and described *Lomatia xeromorpha* (Proteaceae) which had leaves almost identical to an extant Tasmanian endemic, *L. tinctoria*, a shrub typically found in fire prone dry sclerophyll forest. Hill and Christophel (1988) also described *Banksieaeformis dentatus.* This and many other Cethana taxa are allied to *Banksia* and *Dryandra.* These genera now reach their greatest expression in the infertile sandstone soil regions near Sydney and in south-western Western Australia where a Mediterranean climate prevails. *Macrozamia* species are common elements of these floras (Beadle 1981) and in fact, the genus is virtually restricted to siliceous substrates in non-rainforest vegetation (Johnson 1959, 1961). Therefore, it could have occupied a similar low fertility niche in the Early Tertiary in Tasmania, when the climate was everwet.

It is well documented that the cycads, which reached their greatest abundance and diversity in the Jurassic, frequently display xeromorphic characters such as reduced pinnae, heavily thickened cuticles, numerous trichomes, and sunken stomates (Harris 1964; Krasilov 1975). Taxa with these features are often assumed to have reached fossil sites from remote arid regions and the possible importance of edaphic factors in their evolution is not considered. Certain pre-adaptations to less mesic climates and fire derived from evolution in low nutrient soils may have been overriding factors in ensuring the survival of *Macrozamia* through the Tertiary and in the present range of environmental conditions. This general hypothesis was suggested by Beadle (1966, 1981) to explain the development of the widespread Australian sclerophyll flora and has received much support from other researchers (e.g. Johnson and Briggs 1975, 1981; van Steenis 1979; Carpenter and Hill 1988). In Australia we now see a remarkable coexistence of cycads and members of the Proteaceae, Myrtaceae, Leguminosae and Epacridaceae, families which dominate a large proportion of the Australian vegetation. Like many of these angiosperms, *Macrozamia* species possess morphological and physiological strategies which enable them to survive fire (Baird 1977; Burbidge and Whelan 1982), a factor which has undoubtedly become more prevalent in Australia since the arrival of man (Singh *et al.* 1981).

It is also apparent that species of these plants have differentiated through neoteny, though it should be acknowledged that other heterochronic processes may have been involved. Heterochrony is an important factor in macroevolution because it can result in relatively abrupt morphological change with only minimal alteration of the genome (McNamara 1988). Takhtajan (1976), Rothwell (1987) and DiMichele *et al.* (1989) are amongst the few to stress its significance in plant evolution. Regarding cycads, Chrysler (1937) presented evidence that *Stangeria* and tuberous species of *Zamia* are persistent juveniles in habit and some of their vascular tissues. He suggested that these plants evolved in times and regions of climatic stress and hypothesised that similar processes could have occurred in *Macrozamia* and *Encephalartos*, genera which also have both tuberous and trunk-forming species. Johnson (1959) suggested that section *Parazamia* arose relatively recently by a single neotenic divergence but the possibility of one or more other speciation events of this type should be investigated. Anyway, it is not difficult to envisage that heterochrony was significant in the evolution of species of *Macrozamia* during the Late Tertiary and Quaternary. In this period, increasing seasonality and aridity developed as the Australian continent drifted toward the Equator and the polar ice cap developed (Truswell and Harris 1982; Stein and Robert 1986).

Little is known of the comparative ecology of species of the two sections of *Macrozamia*. However, it is noteworthy that Brough and Taylor (1940) have found that pinnae production in *M. communis* is extremely slow and it may take 10–12 years before the juvenile foliage form is lost. Clearly, if it takes this long to reach reproductive maturity, young populations are at risk from repeated fires. On the other hand, if establishment with a fire resistant trunk is attained, and plants can live for several hundred years, then a relatively short fire free period may assure successful regeneration. Section *Parazamia* plants should take much less time to reach reproductive maturity, but it is interesting that their populations are diffuse and produce few cones at irregular intervals (Johnson 1959).

Barber (1965) discussed neoteny in *Eucalyptus*. He suggested that *E. risdonii* maintains the opposite, sessile, highly glaucous foliage characteristic of the juvenile phase of its most closely related species (*E. tenuiramis*) through to reproductive maturity. Specific status is recognised for over 30 such eucalypts and they are usually found in regions of climatic extreme and/or stony and nutrient poor soils (R. J. E. Wiltshire, personal communication). This is of interest since *Eucalyptus* is the usual canopy genus above *Macrozamia* groves and there is evidence that the genus has undergone much expansion during the Quaternary (Singh *et al.* 1981). An intriguing parallel to this possible evolutionary scenario involving *Macrozamia* may be found in South Africa where the closely related genus *Encephalartos* occurs. Over 50 species are known from Africa in a range of habitats including regularly burnt savanna grasslands and arid and rocky alpine regions (Osborne *et al.* 1988; Goode 1989). It is probable that the development of aridity and the effect of anthropogenic fires paralleled that which occurred in Australia (Cowling 1987) and has resulted in the geographic and climatic isolation of *Encephalartos* populations and subsequent speciation. It is also well known that there is also a low sclerophyllous Proteaceae dominated vegetation (fynbos) confined to infertile soils in the South African Cape region. The ranges of several *Encephalartos* species overlap with these communities.

All Australian genera of the Zamiaceae have now been identified from Tertiary sediments of south-eastern Australia. As for some other gymnosperms (Wells and Hill 1989) it is likely that the extinction of cycads from this region was associated with the effects of repeated glaciations in the Late Tertiary and Quaternary, and competition from angiosperms.

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Evolution of Acmopyle and Dacrycarpus (Podocarpaceae) Foliage as Inferred from Macrofossils in South-eastern Australia.

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Abstract

Macrofossil specimens of Dacrycarpus and Acmopyle from south-eastern Australia are investigated. The specimens previously assigned to D. praecupressinus are revised, with one placed in a different genus and new species, Podocarpus witherdenensis, and some placed in a new species, D. latrobensis. One specimen is retained as the lectotype of D. praecupressinus. Dacrycarpus eocenica is re-examined and it is concluded that this species is not Dacrycarpus, but probably belongs to an extinct podocarpaceous genus. Dacrycarpus setiger is transferred to Acmopyle, and three new Acmopyle species, A. florinii, A. glabra and A. tasmanica, are described. It is hypothesised that during the Tertiary in south-eastern Australia stomatal distribution was reduced on Dacrycarpus and Acmopyle foliage. In Dacrycarpus the bilaterally flattened foliage type (which has a greater photosynthetic area than the bifacially flattened foliage) became rare or extinct after the Early Oligocene, prior to the extinction of the genus in the region. Acmopyle has not been recorded in the region after the Early Oligocene. A trend towards reduction in leaf size at high latitudes has previously been demonstrated in angiosperms, but not gymnosperms, and along with the reduction of stomatal distribution, probably represents convergent evolution in response to climatic change.

Introduction

The Podocarpaceae is well represented in the fossil record of south-eastern Australia both as macrofossils and pollen grains. Macrofossils are usually vegetative twigs (Selling 1950; Cookson and Pike 1953a, 1953b; Townrow 1965; Blackburn 1981; Greenwood 1987; Wells and Hill 1989b), but reproductive structures have also been described (Ettingshausen 1886,1888; Greenwood 1987).

The most common podocarpaceous genus in Tertiary sediments in south-eastern Australia is Dacrycarpus (Table 1), which is known from several Tertiary localities in the region (Fig. 1). Most extant Dacrycarpus species exhibit foliar dimorphism. de Laubenfels (1969) notes that in the juvenile form Dacrycarpus leaves are distinctly flattened bilaterally and often spread out distichously, but this character is usually lost in the adult form where bifacially (i.e. dorsiventrally) flattened leaves predominate. However, bilaterally flattened leaves cannot be considered as exclusively juvenile, because many species produce this foliage well after they have reached maturity, and in some (e.g. D. dacrydioides from New Zealand), both foliage types are common throughout the life of the tree. Dacrycarpus compactus from New Guinea is unique among extant species in the genus in producing only bifacially flattened leaves (de Laubenfels 1969; Wells and Hill 1989a).

Both Dacrycarpus foliage types have been described from Australian Tertiary sediments, but the majority of specimens and species only have the bifacially flattened type (Table 1). Specimens with bilaterally flattened foliage have been described as D. praecupressinus from Vegetable Creek (Ettingshausen 1886, 1888), the Latrobe Valley coal, and Bacchus Marsh (Cookson and Pike 1953a, Table 1). Dacrycarpus eocenica from Anglesea was described by Greenwood (1987) as having bilaterally and bifacially flattened foliage, but his illustrations and description are not consistent on this point (see later discussion).

Acmopyle is a distinctive genus, characterised by having the seed fused with the epimatium and an inverted ovule, which gradually becomes nearly erect as it matures (de Laubenfels 1969; Smith 1979). The foliage is also distinctive: the leaves on each short shoot are bilaterally flattened and distichous (Fig. 16), a feature shared with Falcatifolium and one of the foliage types of Dacrycarpus (Smith 1979). It is important

to note that the leaf surfaces referred to for bilaterally flattened foliage of both Dacrycarpus and Acmopyle are the functional leaf surfaces unless otherwise stated. Because of the way in which these leaves are flattened, each functional leaf surface is made up of both adaxial and abaxial leaf surfaces.

The cuticular morphology of extant Acmopyle is unique. The leaves are amphistomatic, with a broad stomatal band on each side of the mid-vein on the underside (non-exposed) leaf surface, and sometimes also across the mid-vein to some degree. The upper (exposed) leaf surface has only a few stomates at the base and apex of the leaf, although this is quite variable. However, between these stomates are zones exhibiting hypoplastic features of stomatal development. This feature was noted by Florin (1931, 1940a), but has since been ignored. Stockey and Ko (1987) examined the cuticular micromorphology of A. pancheri, and showed it to be very distinctive in comparison with the other podocarpaceous species they examined. The bilaterally flattened foliage of Acmopyle and Dacrycarpus can be very difficult to distinguish on gross morphology, although de Laubenfels (1969) notes that a short shoot of Acmopyle never produces a second cycle of leaves (i.e. another vegetative short shoot), but commonly continues into fertile shoots. However, bilaterally flattened short shoots of Dacrycarpus are frequently followed by another short shoot from the apex. In contrast to Dacrycarpus, Acmopyle macrofossils have not previously been recorded from Australia.

This study aims to re-examine specimens previously assigned to Dacrycarpus praecupressinus, D. setiger and D. eocenica, to describe new specimens of Dacrycarpus and Acmopyle, and to interpret foliage evolution of these genera during the Tertiary in south-eastern Australia.

Material and Methods

Specimens were photographed using reflected light with an Olympus OM4 camera with bellows. Cuticles were prepared by soaking leaf fragments in hydrofluoric acid to remove siliceous particles, followed by 10% chromium trioxide until all organic matter except the cuticle was dissolved. Some cuticle was mounted on aluminium stubs using double-sided adhesive tape and air dried. Stubs were coated in a high vacuum evaporative coating unit to a maximum thickness of 20 nm, and examined with a Philips 505 Scanning Electron Microscope operated at 15 kV. The remaining cuticle was neutralised in 5% ammonia, stained with 1% aqueous safranin O, and mounted on microscope slides in phenol glycerine jelly. Cuticles of living species were prepared in the same way.

All specimens from Buckland were believed to have been lost, but a recent search of collections in the Department of Plant Science, University of Tasmania, led to the recovery of several microscope slides and a small amount of sediment. Some of the sediment was used for a palynological preparation in an attempt to refine the age determination, with the remainder being analysed for dispersed cuticle content. All the type specimens from Buckland are still missing.

The fossils described here come from nine localities (Fig. 1), which in chronological order are:

1. Lake Bungarby (36°09'S, 149°08'E). The site is described in detail by Taylor et al. (1990) who assigned the palynoflora to the Upper Lygistepollenites balmei Zone of Stover and Partridge (1973), which encompasses the Late Palaeocene.

2. Regatta Point (42°10'S, 145°20'E). The palynoflora was placed by M.K. Macphail (in Bigwood and Hill 1985) in the Malvacipollis diversus Zone of Stover and Partridge (1973), which encompasses the Early Eocene.

3. Buckland (42°41'S, 147°20'E). The Buckland mudstone was mostly found loose in the Tea Tree Rivulet bed, but some was found in situ (Townrow 1965). On the basis of the palynoflora, Townrow (1965) considered the probable age of the sediment to be Eocene. This has since been refined by M.K. Macphail (pers. comm.), who considers the palynoflora to be late Early Eocene, and more recent than that at

Regatta Point.

4. Anglesea (38°25'S, 144°11'E). The Anglesea site is described in detail by Christophel et al. (1987), who confirmed the late Middle Eocene age determined earlier by palynostratigraphy.

5. Loch Aber (41°02'S, 147°58'E). The palynoflora was assigned by M.K. Macphail (in Hill and Christophel 1988) to the Lower Nothofagidites asperus Zone of Stover and Partridge (1973), which spans the Middle and Late Eocene.

6. Vegetable Creek. The collections assigned to this name by Ettingshausen (1888) come from several sites in the vicinity of Emmaville in northern New South Wales (Fig. 1). The specimens considered here are from Witherden's Tunnel (near GR582425 on the Emmaville 1:50 000 sheet), where the fossils are organically preserved in a brown-grey mudstone. M.K. Macphail (in Hill 1988) assigned the palynoflora from Witherden's Tunnel to the Late Eocene.

7. Cethana (41°32'S, 146°07'E). The gymnosperm and Nothofagus dominated palynoflora was considered by Carpenter and Hill (1988) to encompass the Late Eocene to Oligocene. Further palynological work has identified Cyatheacidites annulatus, Periporopollenites vesicus and Gothanipollis bassensis (S.M. Forsyth pers. comm.). The combined presence of these species is consistent with the Lower to Middle Proteacidites tuberculatus Zonules of Stover and Partridge (1973) for the Gippsland Basin, which corresponds to an Early Oligocene age.

8. Yallourn (38°12'S, 146°21'E). Cookson and Pike (1953a) regarded the coal containing Dacrycarpus praecupressinus to be widespread in the Yallourn coal seam, and Blackburn (1985) reported that the species was widespread in both the Yallourn and Morwell coal seams. This coal ranges in age from Late Oligocene to Miocene, and possibly into the Pliocene (Stover and Partridge 1973).

9. Bacchus Marsh (37°41'S, 144°26'E). Cookson and Pike (1953a) reported Dacrycarpus praecupressinus in a sandy layer on top of the coal at the Lucifer Mine, Bacchus Marsh, to which they assigned a probable Oligocene age (Cookson and Pike 1954).

Dacrycarpus macrofossils

Wells and Hill (1989a) considered the leaf and cuticular morphology of the imbricate leaved genera of the Podocarpaceae in detail and listed diagnostic generic features. During the course of this study some fossils were considered to belong to Dacrycarpus on the basis of Wells and Hill's findings and the diagnostic characters are not repeated here. However, some fossils previously assigned to Dacrycarpus were re-investigated and in some cases their affinities with that genus are questionable. Those fossils are discussed in detail.

Anglesea

Greenwood (1987) described Dacrycarpus eocenica from the Middle Eocene Anglesea sediments on the basis of leafy short shoots. According to Greenwood this species bore long, loosely imbricate, bifacially flattened leaves as well as bilaterally flattened leaves. Wells and Hill (1989b) noted that although Greenwood considered the leaves to be hypostomatic (stomates restricted to the abaxial leaf surface) his illustrations show them to be epistomatic (stomates restricted to the adaxial leaf surface). Several specimens of D. eocenica were supplied to us by Dr D.C. Christophel, and examination of them has confirmed their epistomatic nature.

Based on an examination of these specimens and Greenwood's illustrations, the presence of two foliage types cannot be confirmed with certainty. Larger leaves may become bilaterally flattened, but this may also be due to flattening of spirally arranged foliage during fossilisation. The stomatal and epidermal cell morphology of D. eocenica is typical of Dacrycarpus (Figs 2,3), but there is one striking feature of the leaf morphology which is not. The leaves of D. eocenica have a highly developed marginal frill (Figs 4,5), and D.R. Greenwood (pers. comm.) has confirmed that this

is also present on the holotype. Wells and Hill (1989a) note that a marginal frill is absent from all extant Dacrycarpus species, and none of the fossil Dacrycarpus species observed have one. A marginal frill is common in some other podocarpaceous genera, but D. eocenica is distinct from all of them on the basis of other cuticular characters. We therefore conclude that the fossils assigned to D. eocenica probably do not belong to Dacrycarpus, or to any other extant genus. They may be representatives of an extinct genus, but more comparative work and a re-examination of the holotype is required to confirm this.

Vegetable Creek

Ettingshausen (1886,1888) described Podocarpus praecupressina (transferred to Dacrycarpus by Greenwood (1987)) on the basis of three specimens. Only two of these specimens were fully illustrated (along with a single leaf of the third), and these two specimens were located in the collections of the Geological Survey of New South Wales. One specimen (F 51245, Fig. 6) consists of two short shoots of bilaterally flattened, distichous leaves (presumably two seasons' growth). The leaves on the short shoots are bilaterally flattened, falcate and then curved forward so that the apiculate tip is oriented more or less parallel with the shoot, in the manner described for extant Dacrycarpus foliage by de Laubenfels (1969, 1988). Although there are size differences among the bilaterally flattened foliage of extant Dacrycarpus species, they cannot be separated easily on leaf form alone (Offler 1984), so it is difficult to be specific about the affinities of this fossil. This specimen cannot be Acmopyle, since one short shoot arises from the apex of another, a condition not present in that genus (de Laubenfels 1969). Therefore there is little doubt that this specimen is Dacrycarpus, despite its lack of organic preservation. The other specimen (MMF 1201, Figs 42,43), with a female cone attached, has cuticle preserved on the leaves and is not Dacrycarpus (see later discussion). The species diagnosis provided by Ettingshausen (1886,1888) combines features of the Dacrycarpus foliage and the non-Dacrycarpus reproductive structure.

Since Ettingshausen did not designate a holotype, a lectotype must be designated before D. praecupressinus can be examined further. The original description is based approximately equally on the two specimens, but Ettingshausen (1888) clearly noted the alliance of the fossil species with living species that are now assigned to Dacrycarpus. Therefore he placed most weight on the vegetative specimen (Fig. 6). We designate this specimen as the lectotype of Dacrycarpus praecupressinus.

Yallourn and Bacchus Marsh

Cookson and Pike (1953a) described well preserved specimens from Yallourn and Bacchus Marsh and assigned them to Podocarpus praecupressinus Ett. (now Dacrycarpus praecupressinus). They noted that the name was "originally applied to a "form" species (known only from fragmentary impressions)." They designated the Yallourn specimens as hypotypes of P. praecupressinus, claiming that this narrowed the application of the name. However, Cookson and Pike dismissed the Vegetable Creek specimens too lightly. Although fragmentary, they are large and recognisable, and one of the specimens not only has a reproductive structure attached, but also has organically preserved leaves (thus making it a compression, not an impression).

The specimens described by Cookson and Pike (1953a) from Yallourn and Bacchus Marsh are similar to one another in leaf and cuticular morphology, and we consider them to be conspecific. However, the leaves are distinctly shorter and have a much smaller length:width ratio than the lectotype of D. praecupressinus (Fig. 7 cf. Fig. 6), and we consider that they are a distinct species, here named D. latrobensis. The name D. praecupressinus is best reserved for specimens similar in architecture to the lectotype, and lacking organic preservation, until such time as organically preserved specimens are recovered from Vegetable Creek and the cuticular morphology is described.

The bilaterally flattened foliage of D. latrobensis is amphistomatic (Cookson and

Pike 1953a), and Blackburn (1985) recorded fewer stomates on one leaf surface than the other. Those observations are confirmed in this study, and furthermore the surface that contains the fewest stomates has many stomates that are covered by cuticle in a way that possibly rendered them non-functional (Fig. 8).

The normal stomates have a distinctive cuticular micromorphology (Fig. 9). Cuticle on the subsidiary cells is smooth, although it is slightly granular on the polar cells. The flange between the guard and subsidiary cells is well developed and thin, with a distinctly entire margin. Polar extensions are rudimentary or absent. The flange between guard cells is slightly thickened, with no evidence of polar extensions. Cuticle on the guard cell surface is smooth. Cuticle on the epidermal cells is granular, and the flange between epidermal cells is irregularly fringed.

Regatta Point

A Dacrycarpus species with both bifacially and bilaterally flattened foliage is present at Regatta Point. The bilaterally flattened leaves are about the same length as D. latrobensis, but are narrower and more prominently falcate (Figs 10,11). Stomates on these specimens occur in two distinct bands, which run the length of the leaf on either side of the mid-vein on both surfaces. There are slightly more stomates on one leaf surface than the other, and all stomates are fully formed (Fig. 12).

Imbricate, bifacially flattened foliage (Fig. 13) has been found attached to this bilaterally flattened foliage type. The leaf morphology and arrangement, and cuticular micromorphology of this imbricate foliage is inseparable from that of Dacrycarpus mucronatus, which was described from Oligocene sediments in northwest Tasmania by Wells and Hill (1989b). However, D. mucronatus has not been found with bilaterally flattened foliage. While this does not preclude the presence of that foliage type, we conclude that bilaterally flattened foliage was at least rare in D. mucronatus in the Oligocene compared with the Early Eocene, where it is well represented. Therefore it is necessary to emend the diagnosis of D. mucronatus to encompass the presence of bilaterally flattened foliage.

The cuticular micromorphology of this species is very similar to D. latrobensis (Figs 12,14 cf. Fig. 9). However, both the bifacially and bilaterally flattened leaves are morphologically distinct from those of D. latrobensis. These characters, along with the difference in stomatal development, clearly separate these species, although they are probably closely related.

A second Dacrycarpus species at Regatta Point is represented only by imbricate, bifacially flattened foliage (Fig. 15). The foliage is indistinguishable in leaf shape and morphology and cuticular micromorphology from D. linifolius, which was described from Oligocene sediments in northwest Tasmania by Wells and Hill (1989b). The only distinguishing feature is that whereas stomates occur for much less than one third of the leaf length on the abaxial surface of D. linifolius, they occur up to the apex on the abaxial leaf surface of the Regatta Point fossils (Fig. 16). While this difference has important evolutionary implications which are discussed later, they are not considered sufficient to warrant the erection of a new species. The Regatta Point fossils are therefore assigned to D. linifolius, but the specific diagnosis must be emended to accomodate the stomatal distribution on these specimens.

Loch Aber

Several compression specimens of bilaterally flattened Dacrycarpus foliage were recovered from the Middle to Late Eocene sediment at Loch Aber. The foliage is intermediate in morphology between the bilaterally flattened foliage of D. mucronatus from Regatta Point and D. latrobensis (Fig. 17 cf. Figs 7,10,11). The stomates occur in two rows on either side of the midvein on each leaf surface, running from the leaf base to apex, and all stomates are fully formed (Figs 18,19). This is identical to D. mucronatus. The cuticular micromorphology is similar to that of D. mucronatus and D. latrobensis (Fig. 19 cf. Figs 9,12,14). These specimens cannot be separated from D. mucronatus, and are considered to be conspecific with it. They are similar to D.

latrobensis, differing mainly in the stomatal distribution and development. Because of the similarity of bilaterally flattened foliage across many Dacrycarpus species, it is difficult to determine the specific affinities of fossils in the absence of bifacially flattened foliage.

Cethana

Bilaterally flattened Dacrycarpus foliage similar to that of D. mucronatus from Regatta Point and D. latrobensis occurs at Cethana. Only one specimen has organic preservation, and on it stomates occur all over both leaf surfaces as in D. mucronatus and therefore these specimens are assigned to that species. Bifacially flattened foliage of D. mucronatus has not yet been found at Cethana.

Acmopyle macrofossils

Unlike Dacrycarpus, very little work has been carried out on the cuticular morphology of Acmopyle, and so it was necessary to closely examine the living species, A. pancheri from New Caledonia (Fig. 20) and A. sahniana from Fiji, before the fossils could be properly described. We conclude that the cuticular morphology of this genus is unique. Our examination of the two extant species, confirmed Florin's (1931, 1940a) report of the presence of partially formed stomates on one leaf surface in A. pancheri, and demonstrates it for the first time in A. sahniana (Fig. 21 cf. Fig. 22). This feature has not been observed in other podocarpaceous genera. Another unique feature in the Podocarpaceae, which has not been recorded previously, is the presence of numerous unicellular trichomes on the leaves of A. sahniana (Fig. 23). All specimens of A. pancheri examined were glabrous. Stockey and Ko (1987) examined the cuticular micromorphology of A. pancheri, and showed it to be very distinctive. We have examined the cuticular micromorphology of both extant species, and conclude that Stockey and Ko's specimen was an extreme form of A. pancheri, but there are still some unique micromorphological features of the cuticle. The most obvious and consistent of these is the very granular inner cuticular surface of all epidermal and subsidiary cells (Fig. 24). The stomatal apparatus is also very distinctive under the light microscope, with the wall between the guard cells being very difficult to distinguish, even in fully formed stomates (Fig. 22).

Specimens which share a number of these morphological features have been recovered from five deposits in south-eastern Australia. All have bilaterally flattened foliage, and all specimens examined have the granular inner cuticular surface (the Buckland specimens were not well enough preserved to observe this feature) and indistinct cell walls between the guard cells. Specimens from Lake Bungarby and Buckland have unicellular trichomes which are morphologically identical to those on A. sahniana, but those from Regatta Point, Cethana and Loch Aber are glabrous. Specimens from Regatta Point, Buckland and Cethana exhibit large areas of partially formed stomates, which, among the living podocarps, is unique to Acmopyle. The Lake Bungarby specimens have stomatal rows on either side of the midvein over the entire leaf length on both leaf surfaces, and no partially formed stomates were observed. The Loch Aber specimen had stomates confined to a single row on one leaf surface, and on the other leaf surface there were no fully or partially formed stomates. However, the other features of these specimens were consistent with Acmopyle, and the stomatal distribution appears to be part of an evolutionary series which is discussed in detail later.

Therefore all these specimens are morphologically consistent with Acmopyle, and are referred to that genus. The Lake Bungarby, Regatta Point, Loch Aber and Cethana specimens are all newly discovered. The Buckland specimens were first described by Townrow (1965) as Podocarpus setiger, with the specific epithet being in recognition of the unicellular trichomes. Townrow suggested that P. setiger had a close affinity with living species in Podocarpus section Dacrycarpus. This section has since been elevated to generic rank, and on the basis of Townrow's observation Greenwood (1987) transferred the specimens to the genus Dacrycarpus. We believe that these

specimens belong to the genus Acmopyle, and henceforth refer to them as A. setiger.

Acmopyle macrofossils

Buckland

The type specimen of A. setiger and other species described by Townrow from Buckland are lost, and the deposit no longer exists. However, a leaf fragment and several cuticle slides of A. setiger were available for detailed examination. Townrow (1965) illustrated and described more complete specimens, which are clearly bilaterally flattened, with leaves which are straight or slightly falcate.

The stomates of A. setiger occur in two well defined bands on one leaf surface (Fig. 25), extending from the leaf base to apex. On the other leaf surface stomatal rows are rare or absent on the basal half of the leaf, and in the apical half few stomates are present. However, there are many partially formed stomates (Figs 26, 27). The cuticle is uniformly relatively thick over the leaves. The cuticular micromorphology of A. setiger is unknown, since the cuticle is too degraded to provide the detail required for scanning electron microscope investigation. On the abaxial leaf margin heavily cutinised, unicellular trichomes are prominent (Fig. 28). Cells at the leaf margins of A. setiger are not morphologically distinct from normal epidermal cells.

Lake Bungarby

Three specimens of Acmopyle have been recovered from the Lake Bungarby sediment. The best specimen consists of an entire short shoot, clearly illustrating the bilaterally flattened and distichously arranged leaves (Fig. 29). The cuticle is fragmentary, but individual fragments are well preserved, and enough have been observed to reconstruct the stomatal arrangement and distribution. Stomates are in two bands up to four rows wide on either side of the main vein, and run for the entire leaf length on both leaf surfaces. All stomates are fully developed (Fig. 30), and have thickened lateral subsidiary cells. Cuticle is thin on both leaf surfaces, and leaf margins are marked by a zone of long, narrow, heavily thickened cells. Heavily cutinised, unicellular trichomes are common near the leaf base over the midvein, and along the leaf-bearing axis (Fig. 31).

Cuticle on all subsidiary cells is granular (Fig. 30). The flange between the guard cells and subsidiary cells is well developed, smooth and relatively entire-margined. Polar extensions are very well developed (Fig. 30). The flange between guard cells is thickened, with thin polar extensions. Cuticle on the surface of the guard cells is smooth. Cuticle on the epidermal cells is granular, and the flange between epidermal cells is poorly formed and not fringed (Fig. 30). This combination of characters has not been observed in other Acmopyle species, and therefore these specimens are assigned to a new species, A. florinii.

Regatta Point

A single short shoot of bilaterally flattened Acmopyle foliage has been recovered from Early Eocene sediments at Regatta Point (Fig. 32). The specimen resembles A. florinii in leaf size and shape, but differs in several important cuticular characters. The Regatta Point specimen has two well defined stomatal bands comprising about four rows on one leaf surface (Fig. 33), which has relatively thin cuticle. On the other leaf surface, which has thicker cuticle, stomatal bands are not well defined, and contain a large number of partially formed stomates (Figs 34,35). The leaf margins in this specimen are not well defined, and the leaves are glabrous. This contrasts with the stomatal development and distribution on A. florinii, where it was not possible to differentiate between the two leaf surfaces.

The cuticular micromorphology of the Regatta Point specimen is similar to A. florinii, except that the flange between the guard and subsidiary cells is not as well developed and the polar extensions are wider, and more continuous with this flange (Fig. 36). The Regatta Point specimen is distinct from all Acmopyle species, and therefore is assigned to a new species, A. glabra.

Cethana

Several short shoots of Acmopyle foliage have been recovered from the Early Oligocene Cethana deposit (Fig. 37). Cuticle is well preserved in patches, but is fragmentary, making stomatal distribution difficult to determine. However, stomates are common on one leaf surface but infrequent on the other, and partially formed stomates occur on the surface containing fewest stomates. In these characters the Cethana specimens are similar to A. glabra and A. setiger, although they clearly have less stomates on the "upper" surface than either of those species. The Cethana specimens are distinct in the degree of development of the cuticular flange between the guard and subsidiary cells (Fig. 38), but we do not consider a sufficient distinction to warrant separation into a new species. Trichomes have not been recorded from the Cethana specimens, and given the large number of fragments observed they can be regarded as glabrous. Whilst these specimens are morphologically similar to both A. glabra and A. setiger they are here assigned to A. glabra because of the absence of trichomes. However, new specimens from this deposit may provide more accurate information on stomatal distribution in particular and the Cethana specimens may prove to be a distinct species.

Loch Aber

A single leaf of Acmopyle has been recovered from the Loch Aber sediment. The leaf is about 7mm long and about 1.5mm wide, and is falcate and bilaterally flattened. Stomates occur in a single broad band (up to 12 rows wide) on one leaf surface (Fig. 40), covering approximately the apical two thirds of the leaf. This stomatal band must cover the mid-vein, the position of which cannot be determined accurately. On the other leaf surface, stomates are absent, and there are no partially formed stomates (Fig. 39). The stomatal micromorphology is consistent with that described for Acmopyle, and it is notable that the guard cells are deeply sunken in comparison with the epidermal cells, which in turn are heavily cutinised (Fig. 41). This is very similar to the cuticle of A. pancheri illustrated by Stockey and Ko (1987). Trichomes are absent from the leaf. Therefore, although this leaf has affinities with Acmopyle, it is clearly distinct from all other fossil and living species in its stomatal development and distribution. It is assigned to a new species, A. tasmanica.

Podocarpus sp. nov.

The fertile specimen from Vegetable Creek (MMF 1201, previously Dacrycarpus praecupressinus) consists of a leafy shoot with a mature female cone and possibly an immature cone on another branch (Figs 42,43). The cone consists of a solitary seed enclosed by the ovuliferous scale, with a slightly swollen structure (the receptacle) at the base. This cone type is typical of Dacrycarpus, Nageia and Podocarpus (de Laubenfels 1988). The foliage is arranged spirally, and the leaves have a distinct petiole and midvein. These characteristics rule out Nageia section Nageia, which usually has an opposite leaf arrangement and always has several prominent parallel veins rather than a single midvein, and Dacrycarpus, which either has bilaterally flattened, spreading foliage or bifacially flattened imbricate foliage. However, on the basis of cone and gross leaf morphology and preservation, it is impossible to determine whether the fossil belongs to Podocarpus or Nageia section Polypodiopsis (genus Retrophyllum according to Page (1988)).

The leaf cuticular micromorphology of the fossil assists in determining its generic affinity. The epidermal cells around the stomatal bands are almost straight-walled (Fig. 46), while those over the veins are sinuous and slightly buttressed (Fig. 45). Also, the stomates occur in loose rows, widely separated by epidermal cells on both leaf surfaces. These are features of some species of Podocarpus (Fig. 44) but not Nageia section Polypodiopsis, which has straight epidermal cell walls.

Therefore the fossil is most similar to living species of Podocarpus and is assigned to that genus. Podocarpus is a large genus, and only about 30% of extant

species were observed in this study. The fossil is distinct from those species, and is assigned to a new species, P. witherdenensis.

There are two subgenera of Podocarpus (de Laubenfels 1985),which are recognised by two characters - the presence or absence of two foliola (lanceolate bracts) at the base of the female receptacle, and the presence or absence of Florin rings around the stomates. Furthermore, seeds of most species in subgenus Podocarpus have a crest on the distal end of the seed coat, a feature lacking in subgenus Foliolatus. It is impossible to tell whether foliola are present or absent on P. witherdenensis, but it has poorly defined Florin rings (Fig. 47) which are similar to those produced by some species in subgenus Foliolatus (e.g. P. neriifolius, Fig. 48). There is no crest on the seed, which is consistent with an affinity with subgenus Foliolatus. Therefore the fossil species is assigned to this subgenus, but lack of information on the two foliola renders this uncertain.

Systematics
Order CONIFERALES
Family PODOCARPACEAE
Dacrycarpus (Endlicher) de Laubenfels
Dacrycarpus praecupressinus (Ett.) Greenwood, Aust. J. Bot. 35: 111-33 (1987)
Synonym: Podocarpus praecupressina Ettingshausen, Denkschr.Math.-Nat. Wissen. 53: 81-142 (1886)
Emended diagnosis. Foliage dimorphic; distichous leaves bilateral, falcate, decurrent, strongly keeled with a single, prominently raised vein. Leaf length:width ratio 6:1 - 8:1. Short shoot about 3 cm long, <2 cm wide.
Lectotype. F 51245, designated herein, housed in the Geological Survey of New South Wales, Sydney.
Type locality. Witherden's Tunnel, New South Wales.

Dacrycarpus latrobensis R. Hill & Carpenter, sp. nov.
Synonyms: Podocarpus praecupressinus Cookson and Pike, Aust. J. Bot. 1: 71-82 (1953)
Dacrycarpus praecupressinus Greenwood, Aust. J. Bot. 35: 111-33 (1987)
Diagnosis. Foliage dimorphic; distichous leaves bilateral, straight or somewhat falcate, decurrent, strongly keeled with a single vein. Leaf length:width ratio 2.5:1 - 5:1. Short shoot about 2cm long x 5mm wide. Bifacial leaves small, awl-shaped, spirally arranged, amphistomatic, stomates confined to 2 more or less continuous bands on each surface, those on the adaxial surface being narrower and sometimes shorter than those on the abaxial surface. Bilateral leaves amphistomatic, two longitudinal bands of stomates occurring from leaf base to apex on each surface. Stomates less frequent on one leaf surface, stomates often occluded with cuticle on that surface. Cuticle on lateral subsidiary cells smooth, more granular on polar subsidiary cells. Flange between guard and subsidiary cells well developed, thin, entire-margined. Polar extensions rudimentary or absent. Flange between guard cells slightly thickened, no polar extension.
Holotype. P 15714, housed in the Museum of Victoria, Melbourne.
Type Locality. Yallourn, Victoria.
Etymology. Named for the Latrobe Valley coal, which contains abundant specimens of this species.
Specimens Examined. P 15713-15715 (Yallourn), P 15716 (Bacchus Marsh).
Discussion. Cookson and Pike (1953a) provided a detailed description of this species, but only a few of the characters are diagnostic. The remainder of their discussion of the morphology of the species is not repeated here.

Dacrycarpus mucronatus Wells & Hill, Aust. Syst. Bot. 2: 387-423 (1989)
Emended diagnosis. Bifacially flattened leaves spirally arranged, narrow to falcate, decurrent, imbricate, appressed, strongly keeled, 1.9 (1.3-2.7) mm long, 0.4 (0.3-

0.5) mm wide, apex mucronate, incurved. Leaf base contracted, about 0.2 mm wide. Margins entire. Cuticle amphistomatic; stomates in four distinct zones, two narrow bands either side of midvein on both surfaces, extending to apex on adaxial surface. Stomates in uniseriate rows, sometimes disordered or discontinuous or merging with others, rows parallel with long axis of leaf and typically separated by 1-3 epidermal cells; stomates absent near leaf margin, across midvein, across abaxial surface. Stomatal zone 1-4 rows wide (typically 2-3). Stomates unequally amphicyclic, encircling cells usually missing from polar regions, often spanning adjacent subsidiary cells in lateral regions; polar subsidiary cells typically shared between adjacent stomates in a row, square or rounded with smooth anticlinal walls or granular periclinal walls; lateral subsidiary cells crescentic with a thick band of cuticle displaying prominent lateral and polar extensions adjacent to the guard cell, periclinal walls granular to smooth. Polar subsidiary cells 2, lateral subsidiary cells 2-4. Stomatal apparatus normally ovate, sometimes irregular. Stomatal pore elongate, orientation parallel to the long axis of the leaf, 20x7 um. Florin rings indistinct, sunken below leaf surface. Epidermal cellls within stomatiferous zones square to rectangular, irregular, shorter than non-stomatiferous epidermal cells. Non-stomatiferous epidermal cells are narrow parallelograms forming rows parallel to long axis of leaf, anticlinal walls thin, smooth, sometimes pitted, periclinal walls flat, granular. Distichous leaves, if present, bilaterally flattened, falcate, decurrent, strongly keeled with a single vein. Leaf length:width ratio about 5:1. Leaves amphistomatic, with two longitudinal stomatal bands occurring with approximately equal frequency from leaf base to apex on each surface.
Discussion. The diagnosis has been emended to incorporate specimens from three deposits, Regatta Point, Loch Aber and Cethana which have bilaterally flattened foliage. This foliage type was not observed among specimens examined when the original species diagnosis was written. The new specimens examined are: RPE-016, 060-063, LA-033 and C-052, 203, 619, which are housed in the Department of Plant Science, University of Tasmania.

Dacrycarpus linifolius Wells & Hill, Aust. Syst. Bot. 2: 387-423 (1989)
Emended diagnosis. Foliage uniform, spirally arranged; leaves bifacial, decurrent, imbricate, closely appressed, distinctly linear, keeled, 4-5mm long, 0.5-0.7mm wide at broadest point, tapering to acute apex, base constricted, 0.2-0.4mm wide. Margin entire. Apex straight or curved outwards. Cuticle amphistomatic, stomates in four distinct zones, two narrow bands on each side of wide stomate free zone across midvein on both leaf surfaces, nearly extending as far as apex on adaxial surface, variable on abaxial surface. Stomates in uniseriate rows, sometimes discontinuous or merging with others; rows parallel to longitudinal leaf axis, sometimes with stomates in contact or separated by 1-3 rows of epidermal cells. Stomatal zone 1-3 rows wide. Stomates extremely elongated, paratetracytic; polar subsidiary cells 2, square to rounded, often shared between adjacent stomates of a row; periclinal walls granular; lateral subsidiary cells 2, rarely divided, narrow rectangular to narrow crescent shaped, periclinal walls smooth to granular. Cuticular flange between guard cells and subsidiary cells elongate with distinct polar and lateral extensions, the latter sometimes reaching the opposite wall of lateral subsidiary cell. Subsidiary cell outer anticlinal walls deeper than epidermal cell anticlinal walls. Stomatal pore elongate, 18-25um long. Florin ring absent or very indistinct. Epidermal cells rectangular, arranged in longitudinal files, sometimes shorter within stomatiferous zones, granular flat periclinal walls, thin, smooth, sometimes pitted anticlinal walls. Anticlinal walls on abaxial surface often with lateral extensions covering the wall from sight under SEM.
Discussion. The orignal specimens on which this species was based had stomates restricted to approximately the basal third of the leaf on the abaxial surface. The specimens examined during this study, from Regatta Point (specimen numbers RPE-064,070,211,962) have stomates over the entire abaxial leaf surface.

Acmopyle Pilger
Acmopyle florinii R. Hill & Carpenter, sp.nov.
Diagnosis. Foliage dimorphic; distichous leaves bilateral, falcate, decurrent, strongly keeled with a single vein. Leaf length:width ratio 8:1 - 10:1. Short shoot about 4cm long, 2cm wide. Leaves amphistomatic, two longitudinal bands of stomates occurring from leaf base to apex on each surface. Cuticle in stomatal bands relatively thin, cells at leaf margin relatively long, narrow and heavily cutinised. Cuticle on all subsidiary cells granular. Flange between guard and subsidiary cells well developed, smooth, relatively entire-margined. Polar extensions well developed. Flange between guard cells well developed, with thin polar extensions. Heavily cutinised, unicellular trichomes arising from a single foot cell occur sparsely over midvein, becoming more frequent towards leaf base, and common over the leaf-bearing axis.
Holotype. LB-063, housed in the Department of Plant Science, University of Tasmania.
Type locality. Lake Bungarby, New South Wales, Australia.
Etymology. Named for Rudolf Florin, who first noted the unusual stomatal development in Acmopyle, and made a major contribution to the study of Southern Hemisphere fossil and living gymnosperms.
Specimens examined. LB-046, 063, 096.

Acmopyle glabra R. Hill & Carpenter, sp.nov.
Diagnosis. Leaves distichous, bilaterally flattened, falcate, decurrent, strongly keeled with a single vein. Leaf length:width ratio 6:1 - 8:1. Short shoot up to 4cm long, 1.6cm wide. Leaf irregularly amphistomatic. On one leaf surface stomates in two orderly bands running from leaf base to apex, cuticle relatively thin. On the other surface stomates in two discontinuous bands, interrupted by many hypoplastic stomates, cuticle relatively thick. Cuticle on all subsidiary cells granular. Flange between guard and subsidiary cells well developed, smooth, relatively entire-margined. Polar extensions well developed, wide, continuous with flange between guard and subsidiary cells. Flange between guard cells well developed, with thin polar extensions. Leaf glabrous.
Holotype. RPE-006, housed in the Department of Plant Science, University of Tasmania.
Type locality. Regatta Point, Tasmania.
Specimens examined. RPE-006, C-222.
Etymology. Named for the absence of trichomes from the species.

Acmopyle setiger (Townrow) R. Hill & Carpenter, comb. nov.
Synonyms: Podocarpus setiger Townrow, Pap. Proc. R. Soc. Tas. 99: 87-107 (1965)
Dacrycarpus setiger (Townrow) Greenwood, Aust. J. Bot. 35: 111-33 (1987)
Emended diagnosis. Distichous leaves bilaterally flattened, straight or slightly falcate, apex acute to mucronate, base contracted. Leaf length about 6 mm (4-8 mm), width 2 mm. Midvein prominent, asymmetrical, lying near abaxial leaf margin, which bears stiff, unicellular trichomes. On one leaf surface stomates in two orderly bands running from leaf base to apex. On the other surface stomates in two discontinuous bands usually restricted to the apical half of the leaf, interrupted by many hypoplastic stomates. Cuticle on both leaf surfaces relatively thick.
Lectotype (here designated). B-001, housed in the Department of Plant Science, University of Tasmania, Australia.
Type locality. Buckland, Tasmania.
Specimens examined. B-001-006.
Discussion. The holotype of A. setiger is missing, and therefore it has been necessary to designate a lectotype from among the remaining specimens from this locality.

Acmopyle tasmanica R. Hill & Carpenter, sp. nov.
Diagnosis. Distichous leaves bilaterally flattened, slightly falcate, apex mucronate,

base contracted. Leaf length about 7mm, width 1.5mm. On one leaf surface stomates in an orderly band about 12 stomatal rows wide running for the apical 2/3 of the leaf. Guard cells deeply sunken in comparison with epidermal cells. Stomates absent from the other leaf surface. Cuticle on both leaf surfaces relatively thick. Leaf glabrous.
Holotype. LA-060, stored in the Department of Plant Science, University of Tasmania.
Type Locality. Loch Aber, Tasmania.
Etymology. Named for the presence of this species in Tasmania.

Podocarpus l'Heritier ex Persoon
Subgenus Foliolatus de Laubenfels
Podocarpus witherdenensis R. Hill & Carpenter, sp. nov.
Synonyms: Podocarpus praecupressina Ettingshausen, Denkschr. Math.-Nat. Wissen. 53: 81-142 (1886)
Dacrycarpus praecupressinus (Ett.) Greenwood, Aust. J. Bot. 35: 111-33 (1987)
Diagnosis. Leaves spirally arranged, 8-9mm long, 2mm wide, with a single prominent midvein. Stomates in poorly defined rows, unequally spaced. Subsidiary cells usually four (paratetracytic), sometimes five. Epidermal cells between stomates and in non-stomatal areas sinuous and slightly buttressed. Florin rings weakly developed, not well defined. Outer leaf surface in stomatal area ornamented with cuticular undulations. Seed borne terminally, enclosed by a thick, modified fertile scale, oval, 10mm long, 7.5mm wide, outline smooth, not noticeably crested. Receptacle small, narrower than seed and tapering quickly to small scales at base. Foliola not observed.
Holotype. MMF 1201, housed in the Geological Survey of New South Wales, Sydney.
Type Locality. Witherden's Tunnel, N.S.W.
Etymology. Named for the locality from which the single specimen was collected.

Discussion
Dacrycarpus

This investigation demonstrates that the complex of specimens previously assigned to Dacrycarpus praecupressinus represents three species in two genera. It has also further confirmed that Dacrycarpus was very diverse in Australia during the Tertiary (Table 1). Dacrycarpus now occurs from southernmost China to Fiji and New Zealand, including Vanuatu and New Caledonia, with the highest diversity in New Guinea, often in relatively cool, high altitude forests. However, the absence of Dacrycarpus in Australia today poses an important ecophysiological problem, which is in need of experimental investigation. It is likely that climatic change in the Tertiary and possibly also associated with Quaternary glaciations led to the demise of Dacrycarpus in Australia, and this could be tested on extant species. Increasing fire frequency associated with the climatic changes may also have been important, as has been suggested for other rainforest gymnosperms (Kershaw 1988).

The affinities of the Dacrycarpus species described here are difficult to determine. Townrow (1965) and Greenwood (1987) noted that D. latrobensis has a similar stomatal distribution to D. dacrydioides (the extant New Zealand species), but the two differ markedly in cuticular micromorphology (see Wells and Hill 1989a). Wells and Hill (1989b) suggested modern affinities for most of the bifacially flattened Dacrycarpus foliage they described, but leaf morphology was an important aid to their conclusions, and bilaterally flattened Dacrycarpus leaves are much less variable than bifacially flattened leaves. It is difficult to nominate morphological characters from Dacrycarpus leaves and their cuticles which differentiate the fossil and living species and which could be useful for cladistic analysis. There is strong evidence for convergent evolution in Dacrycarpus leaf morphology in response to climatic change, and this is presented later. However cladistic analysis of fossil Dacrycarpus leaves will be difficult if it is possible at all and requires a much more exhaustive study of the leaf morphology of living podocarps than has currently been undertaken. This is the subject of ongoing research.

Acmopyle

Florin (1940b) summarised the fossil record of Acmopyle, and there are no more recent reports of the genus from the fossil record. According to Florin (1940a) there is one species, A. antarctica, from Tertiary sediments in Antarctica, and another, A. engelhardti, in South America. Both of these species are represented by foliage impressions only, and cannot be critically compared with the fossils described here. Florin (1940b) notes that a specimen described as Retinosporites indica by Holden (1915) from Jurassic sediments in India "resembles Acmopyle Pancheri so closely, that a close systematic affinity between the two genera must be presumed". However, Florin stopped short of formally transferring R. indica to Acmopyle, and although the cuticular preservation of this specimen is good it will require a detailed re-examination incorporating SEM work to determine its true affinities. Thus there are no fossil species which can be critically compared with those described here, which represent the first macrofossils of the genus with organic preservation.

In foliage morphology the two living species are similar (Buchholz and Gray 1947), although only one specimen of A. sahniana was available to us (according to Smith (1979) only six collections of the species exist). The major difference between the two is that A. pancheri is glabrous, whereas A. sahniana bears numerous unicellular trichomes. The presence or absence of trichomes is not normally considered a rigorous taxonomic character, but their presence in A. sahniana is certainly significant, since they have not previously been observed in the family. Furthermore, identical trichomes to those found on A. sahniana are found on the fossil species A. florinii and A. setiger. Since trichomes are absent from all other fossil and living podocarpaceous genera examined to date it can be stated with confidence that these trichomes represent a derived character in Acmopyle, and that A. florinii, A. setiger and A. sahniana represent a monophyletic group. While the cuticular morphology of Acmopyle is particularly distinctive, few other cuticular characters vary among the fossil and living species and thus there is little scope for further phylogenetic inference. One of the variable characters within the genus is the distribution of stomates on one leaf surface. This can range from total coverage (A. florinii) to total absence (A. tasmanica), with the other species being intermediate in nature. However this character is probably highly convergent in Acmopyle for the following reasons:

1. Within the monophyletic group of species mentioned above there is a range from stomates totally over both leaf surfaces (A. florinii) through to stomates moderately abundant (A. setiger) or sparse (A. sahniana) on one leaf surface. Among the other species stomates are common on one leaf surface and range from moderately abundant (A. glabra from Regatta Point) to sparse (A. pancheri and A. glabra from Cethana) or absent (A. tasmanica) on the other. While these stomatal distributions may not necessarily represent independent phylogenetic lines they do indicate that similar responses were occurring in at least two lines. We conclude that this is convergent evolution in response to changing climate.
2. The two extant species, A. pancheri and A. sahniana, have probably been in separate phylogenetic lines since at least the Late Palaeocene, when A. florinii occurred with the derived character of trichomes on the leaves. Despite this, they have very similar stomatal distributions and occur in very similar climatic belts.

For these reasons it is our view that stomatal distribution should not be used as a character for phylogenetic reconstruction in Acmopyle. Therefore, when only leaf morphology is considered there is only one unambiguous character (presence of trichomes), which has been used to define a monophyletic group of three species.

This research has shown that Acmopyle was relatively widespread in south-eastern Australia during the Early Tertiary, with four species described from Late Palaeocene to Oligocene sediments. The two extant species of Acmopyle occur in New Caledonia and Fiji respectively. The geological history of the southwest Pacific region is of considerable complexity, but it is known that the Fiji islands, along with those of Lau, Tonga, Vanuatu and the Solomons comprise an Outer Melanesian arc system which

apparently formed in the Early Eocene at the eastern margin of the Australian plate (Crook 1981; Colley and Hindle 1984). Prior to this, at approximately 80-60 million years ago the Tasman Sea formed between Australia and New Zealand and the New Caledonia trough formed between the region of New Caledonia and the Lord Howe Rise (Crook 1981). Therefore, Australia may last have had land connection with the Fiji/New Caledonia region in this period through the Queensland Plateau and the Lord Howe Rise (Coleman 1980; Crook 1981). The presence of a complement of land snakes and frogs in Fiji and numerous continental floral elements may be remnants of this connection (Raven and Axelrod 1972). With the discovery of Acmopyle fossils in the Late Palaeocene Lake Bungarby deposit it seems likely that the genus formed part of the rainforests across this region but probably became disjunct at the start of the Eocene, the time that Crook (1981) considers that Fiji last lay relatively close to New Caledonia.

The presence of Acmopyle in Fiji and New Caledonia today is probably due to a continual period of climatic similarity in these regions from the Early Tertiary to the present, particularly of high rainfall and humidity. Acmopyle pancheri occurs in New Caledonian rainforest near sea level (de Laubenfels 1969, 1972) but by far the most collections have been made from the serpentine mountains of the south of the island, which reach an altitude of about 1200 m. Acmopyle sahniana is known only from two mountains of Viti Levu, the main island of Fiji, where it occurs at altitudes of 670-1050 m in dense rainforest or in stunted forest on exposed ridges (Smith 1979). As their altitudinal and latitudinal similarities suggest, the climate of these montane areas of New Caledonia and Fiji are similar. They are frequently enveloped in clouds and are apparently typified by mild equable conditions in which mean annual temperatures are of the order of 13-17°C and relative humidity is very high (Specht 1979; Smith 1979; Schmid 1981; Ash 1988). Southeast trade winds bring moisture laden air to these summits and evenly distributed orographic rainfall may exceed 5000 mm on upper windward slopes (Smith 1979; Schmid 1981). Schmid (1981) notes a positive association between the concentration of ancient plants and high rainfall in New Caledonia. As altitude increases the forests tend to become progressively stunted and feature an abundance of epiphytic orchids, ferns and bryophytes.

In terms of stomatal distribution and development, the extant species most closely resemble the fossil species A. glabra and A. setiger, and this appears to be such a variable characteristic among the fossils that it may prove to be an important climatic indicator (as discussed earlier). That is, the Early Eocene to Early Oligocene climate in Tasmania may have been similar to that which presently occurs in the Fijian and New Caledonian highlands, in rainfall (both amount and distribution throughout the year) at least. The following discussion further considers the importance of leaf form.

Evolution in Dacrycarpus and Acmopyle foliage

The morphology of the Australian macrofossil Dacrycarpus and Acmopyle species suggests trends in foliage evolution which are summarised in Figures 49 and 50. There is strong evidence that this evolution has occurred in several phylogenetic lines in response to climatic change and therefore represents convergence. Documentation of this is important in determining general plant morphological responses to climate change and should also be of benefit to those with an interest in identifying convergence for phylogenetic studies.

There are two fossil Dacrycarpus species which cover a substantial stratigraphic range. The first is D. mucronatus, which is present from the Early Eocene to the Oligocene. The oldest specimens have both bilaterally and bifacially flattened foliage, and stomates are distributed equally over both leaf surfaces. Middle-Late Eocene and Early Oligocene specimens also exhibit bilaterally flattened foliage, with stomates distributed equally over both leaf surfaces. However, Oligocene D. mucronatus from Little Rapid River is known only as bifacially flattened foliage, suggesting that the bilaterally flattened foliage had become rare or absent at that site by that time. It should be noted that among several hundred specimens from three Oligocene localities which

probably post-date Cethana, Wells and Hill (1989b) recorded only one which was bilaterally flattened, and it was too poorly preserved for detailed description. Dacrycarpus latrobensis occurs at a substantially later time, and still has both foliage types. However, stomates are more common on one leaf surface than the other, and on the surface with fewest stomates, many are plugged with cuticle to an extent which possibly rendered them non-functional. Dacrycarpus latrobensis also occurs further north than D. mucronatus or any of the other Tasmanian Oligocene species, and if the loss or substantial reduction of bilaterally flattened foliage was due to climatic change, it may have occurred later at lower latitudes. Therefore, among these species there is evidence for loss of stomates on bilaterally flattened foliage, and in Tasmania at least, loss of the bilaterally flattened foliage type.

The second species with a long stratigraphic range is Dacrycarpus linifolius, which occurs in Early Eocene sediments at Regatta Point and Oligocene sediments at Little Rapid River. This species has only been recovered as bifacially flattened foliage, which in gross leaf morphology is identical at the two sites. However, whereas the Early Eocene leaves have stomates along the entire length of both leaf surfaces, in the Oligocene leaves stomates are restricted to less than the basal third of the abaxial surface. This again provides evidence for reduction in stomatal distribution, but this time on the bifacially flattened leaves.

The remaining Dacrycarpus fossil species do not individually have long stratigraphic ranges, but they do exhibit general trends in leaf morphology. Wells and Hill (1989b) described six Dacrycarpus species from lowland Oligocene sites in Tasmania, and all have imbricate, bifacially flattened foliage. Five of these species are amphistomatic, but in the sixth, D. linearis, stomates are probably restricted to the adaxial surface. Wells and Hill also described three Dacrycarpus species from the high altitude Late Oligocene-earliest Miocene Monpeelyata locality. All these species are epistomatic (stomates restricted to the adaxial surface) and closely imbricate, so that the stomates are concealed. The bifacially flattened foliage of all extant Dacrycarpus species is amphistomatic, although in D. compactus, which occurs at high altitudes in New Guinea, and is the only extant species to lack bilaterally flattened foliage, there are very few stomates on the abaxial surface (Wells and Hill 1989a). However, it is significant that the extant podocarpaceous species Microstrobos niphophilus and Microcachrys tetragona, which occur in alpine vegetation in Tasmania, are also closely imbricate and epistomatic (Wells and Hill 1989a). A similar Microstrobos species co-occurs with Dacrycarpus in the Monpeelyata sediment (Wells and Hill 1989b, Fig. 49), but also occurs in the lowland Oligocene Little Rapid River sediments. Both of these fossils are epistomatic. Thus there seems to have been general convergent evolution within and among podocarpaceous genera towards the restriction of stomates to the adaxial surface in imbricate leaved species. The extant Lagarostrobos franklinii in Tasmania, which also has imbricate leaves, generally occurs at low altitudes along permanent water courses and represents an exception in that it still has stomates on the abaxial as well as the adaxial leaf surface. Oligocene Lagarostrobos fossils from Cethana and Little Rapid River have similar stomatal distributions. Dacrycarpus is now extinct in south-eastern Australia, although palynological evidence suggests that it remained in the region until the Early Pleistocene (Hill and Macphail 1985, 1991).

Among the fossil Acmopyle species described here there is a clear trend in stomatal distribution (Fig. 50) starting with the Late Palaeocene A. florinii, which has fully formed stomates evenly distributed over both leaf surfaces, and no partially formed stomates. The Early Eocene specimens of A. glabra have rows of fully formed stomates on one leaf surface and rows of fully and partially formed stomates covering the length of the other surface. The late Early Eocene A. setiger has rows of fully formed stomates on one leaf surface, but fully formed stomates are restricted to the apical half of the other surface, with partially formed stomates more widespread. The Middle-Late Eocene A. tasmanica has a single, broad row of fully formed stomates on one leaf surface, and no stomates, fully or partially formed, on the other. The stomatal distribution of the early Oligocene A. glabra fossils is less certain, but fully formed

stomates are very uncommon on one surface. The Cethana A. glabra specimens have a wider stomatal distribution than A. tasmanica even though they post-date it. The Cethana specimens are the last recorded occurrence of Acmopyle in south-eastern Australia to date.

The partially formed stomates and stomatal rows may be evidence for stages in either the loss of stomates from one leaf surface or the acquisition of stomates by that leaf surface. Given the incompleteness of the fossil record, no conclusion can be certain at this time, but there is a general stratigraphic trend which is difficult to ignore. It is likely that stomates were being progressively lost from one leaf surface during the Late Palaeocene to Early Oligocene, and this was happening in more than one phylogenetic line.

Both living species of Acmopyle have fully formed stomates in two rows along the entire length of the underside of the leaf. However, on the upper surface stomates are restricted to small areas near the leaf base and apex (Florin 1940b and our observations). Thus they have more restricted stomatal distributions on this leaf surface than in any of the fossil species except A. tasmanica and possibly A. glabra from Cethana, and the partially formed stomates are still present between these stomatal areas.

This restriction in the distribution of stomates on Acmopyle leaves during the period from the Late Palaeocene to the Early Oligocene in southeastern Australia probably occurred in response to climatic changes. Previous research (Hill 1983) has shown a reduction in leaf size in subgenus Menziesospora (Hill and Read 1991) of the angiosperm Nothofagus (Fagaceae) in south-eastern Australia during the Tertiary, starting with the large-leaved N. tasmanica and ending with the extant, small-leaved species in the region, N. cunninghamii. Hill and Read (1987) hypothesised that several other angiosperm tree species in Tasmania arose by a similar reduction in leaf area in response to Tertiary climatic change. This trend is also evident in Dacrycarpus, which reduces or loses its bilaterally flattened foliage during the Early Tertiary in Tasmania at least. However, Dacrycarpus and Acmopyle are different to the angiosperms recorded to date in that they appear to be responding to climatic changes by restricting their stomatal distribution on one leaf surface. Hill (1990) listed a general temperature decline, declining and more seasonal rainfall, a change from predominantly summer to predominantly winter rainfall and declining humidity as important climatic factors in Tertiary plant evolution in the region, and Read et al. (1990) considered the range of temperature extremes to be one of the most important factors influencing species distribution in Australia during the Tertiary.

It is probable that changes in rainfall and evapotranspiration were important for the evolution and extinction of Dacrycarpus and Acmopyle. The restriction of stomatal number and distribution is likely to be a response to a high transpirational load during at least part of the year. Mott et al. (1982) note that the presence of stomates on both leaf surfaces means that there are two boundary layers which act in parallel, and therefore water loss is significantly greater than from an equivalent leaf with stomates on only one leaf surface. Furthermore, evergreen conifers are known to have a relatively low maximum photosynthetic rate (Korner et al. 1979), and therefore the potential photosynthetic advantage in having stomates on both leaf surfaces may not be great. Therefore the simplest hypothesis is that stomates were being restricted on one leaf surface in Dacrycarpus and Acmopyle because the photosynthetic advantage of amphistomatic leaves was outweighed by climatic changes which led to periodically dry conditions and potential drought damage from excessive transpiration. Two complicating factors are:

1. During the Tertiary Australia moved from very high latitudes towards the equator, and consequently there were major changes in photoperiod and light intensity in south-eastern Australia. The effect of this on stomatal distribution is difficult to predict.
2. It has been suggested that CO_2 levels were higher during the Early Tertiary than at present (Berner et al. 1983; Barron and Washington 1984). The effect of this on stomatal distribution is uncertain, although Woodward (1987) reported a decrease in

stomatal numbers in a range of plants in response to increased CO_2 levels over the last 200 years.

Conclusion

There is strong evidence in Dacrycarpus for a reduction in photosynthetic area and in Dacrycarpus and Acmopyle for a restriction in the distribution of stomates during the period from the Early Eocene to the Miocene. These genera are novel for the following reasons:

1) Dacrycarpus is the first gymnosperm in which a reduction in photosynthetic area during the Tertiary in south-eastern Australia has been demonstrated;
2) Dacrycarpus and Acmopyle are the first genera in south-eastern Australia in which there is evidence for a restriction in stomatal distribution during the Tertiary; and
3) despite their ability to evolve apparently in response to climatic change, both genera are now extinct in the region (although fire may also have been a significant factor in this extinction).

There are two lines of evidence to suggest that changes in rainfall and evapotranspiration may have been important for the evolution and extinction of Dacrycarpus and Acmopyle. Firstly, the restriction of stomatal number and distribution is likely to be a response to an excessive transpirational load during at least part of the year, and there is a general trend in all groups of Dacrycarpus and Acmopyle discussed for stomates to be confined to one leaf surface.

Secondly, three Dacrycarpus species have been described from Monpeelyata in central Tasmania. This deposit has been discussed in detail by Macphail et al. (1991) and is considered to be an early example of subalpine vegetation. If temperature was the only limiting factor on Dacrycarpus distribution during the Tertiary then it would be expected that the genus would still be common in Australia, since much of the continent is almost certainly warmer today than Monpeelyata was at the Late Oligocene-earliest Miocene (Macphail et al. 1991).

The last fossil occurrence of Dacrycarpus in south-eastern Australia is pollen from the Early Pleistocene sediments at Regatta Point in western Tasmania (Hill and Macphail 1985, 1991). Dacrycarpus is one of several taxa present in these sediments which are now extinct in Tasmania or in some cases Australia. It is probable that the glacial cycles brought about this extinction, either because of low temperatures, glacial aridity, or a combination of the two. The presence of a living Dacrycarpus species in New Zealand offers a strong parallel for this recent history in Tasmania, except that in that case the species has survived the glaciations and both foliage types are common.

Among the extant species, only D. compactus exhibits marked morphological adaptations to a cooler climate and possibly to periodically high transpiration rates. This species, which occurs up to and above the tree line in New Guinea (Hope 1980), does not have bilaterally flattened foliage, and is virtually epistomatic, with only a few stomates on the abaxial leaf surface. However, many of the adaptations seen among Tertiary Dacrycarpus and Acmopyle species in south-eastern Australia, which presumably were a response to sub-optimal conditions, are absent from extant species, which do not appear to be well adapted for marginal climates. Thus it appears that Dacrycarpus and Acmopyle today are more or less restricted to regions of optimal climate. This may reflect the fact that competition from other plants, and in particular angiosperms, is more intense now than it was during the Early Tertiary and Dacrycarpus and Acmopyle (and possibly many other gymnosperms) are now competitive only where the climate is close to optimal for them.

This study has further demonstrated the utility of the macrofossil record in determining the effect of climate on plant distribution and evolution. Many taxonomic groups remain to be studied in this detail, and they may provide further evidence for the evolution of leaf form in south-eastern Australia to climatic change.

Acknowledgments

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Table 1. Dacrycarpus macrofossils described from Australian Tertiary sediments. (after Ettingshausen (1886,1888), Selling (1950), Cookson and Pike (1953a), Greenwood (1987) and Wells and Hill (1989b)).

Species	Foliage type	Location
Dacrycarpus acutifolius	bifacial	Monpeelyata
D. arcuatus	bifacial	Little Rapid River, Pioneer
D. crenulatus	bifacial	Pioneer
D. cupressiformis	bifacial	Little Rapid River
D. eocenica	bifacial, bilateral	Anglesea
D. involutus	bifacial	Monpeelyata
D. lanceolatus	bifacial	Monpeelyata
D. latrobensis	bifacial, bilateral	Yallourn, Morwell, Bacchus Marsh
D. linearis	bifacial	Little Rapid River
D. linifolius	bifacial	Little Rapid River, Regatta Point
D. mucronatus	bifacial, bilateral	Little Rapid River, Regatta Point, Loch Aber, Cethana
D. praecupressinus	bilateral	Vegetable Creek

FIGURE CAPTIONS

Figure 1. Map of south-eastern Australia showing the localities where macrofossils of Dacrycarpus and/or Acmopyle have been recovered. 1 = Vegetable Creek (Witherden's Tunnel), 2 = Bacchus Marsh, 3 = Anglesea, 4 = Yallourn, 5 = Lake Bungarby, 6 = Little Rapid River, 7 = Pioneer, 8 = Loch Aber, 9 = Cethana, 10 = Regatta Point, 11 = Monpeelyata, 12 = Buckland (= Palaeocene, = Eocene, = Oligocene, = Oligocene-Miocene).

Figures 2-5. Scanning electron micrographs of the cuticle of Dacrycarpus eocenica (AM-4001). Figure 2. Stomatal band on the inner cuticular surface of the adaxial leaf surface. x330. Figure 3. Typical Dacrycarpus-type stomate on the inner cuticular surface of the adaxial leaf surface. x950. Figure 4. Inner cuticular surface showing the adaxial surface with stomatal bands above and the abaxial surface below, with the leaf margin in the centre. Note the diagonally directed cells at the margin which make up the marginal frill. x410. Figure 5. Outer surface of the leaf showing the marginal frill (f) made up of diagonally directed cells. x220.

Figure 6. Lectotype of Dacrycarpus praecupressinus Ett. (F 51245). Two short shoots are present, with the base of the uppermost one arrowed. Scale = 2 mm. Figure 7. Holotype of D. latrobensis (P 15714), showing a complete short shoot attached to a branch. Scale = 2 mm. Figures 8,9. Scanning electron micrographs (SEMs) of the inner cuticular surface of leaves of Dacrycarpus latrobensis. Figure 8. Leaf surface containing fewest stomates, showing stomates occluded by cuticle (P-15713). x650. Figure 9. Leaf surface containg most stomates, showing an apparently fully functional stomate (P-15716). x925.

Figures 10-14. SEMs of Dacrycarpus mucronatus from Regatta Point. Figure 10. Part of a bilaterally flattened shoot (RPE-061). x17. Figure 11. Part of a bilaterally flattened shoot (RPE-060). x17. Figure 12. Inner cuticular surface showing a single, fully formed stomate from bilaterally flattened foliage (RPE-062). x1000. Figure 13. Part of a bifacially flattened shoot (RPE-462). x17. Figure 14. Inner cuticular surface showing a single, fully formed stomate from bifacially flattened foliage (RPE-681). x1000.

Figures 15,16. SEMs of Dacrycarpus linifolius from Regatta Point. Figure 15. Part of a bifacially flattened shoot (RPE-064). x23. Figure 16. Inner cuticular surface showing a stomatal band from the adaxial (lower) and abaxial (upper) surface (RPE-070). The leaf margin is in the centre. x200. Figures 17-19. Bilaterally flattened Dacrycarpus mucronatus foliage from Loch Aber (LA-033). Figure 17. Bilaterally flattened short shoot. Scale = 1 mm. Figure 18. SEM of the inner cuticular surface showing part of a stomatal row. x300. Figure 19. SEM of the inner cuticular surface showing a single stomate. x900.

Figure 20. Short shoot of Acmopyle pancheri. Scale = 1 cm. Figure 21. Cuticle from the upper leaf surface of A. sahniana, showing a fully formed stomate (left) and a hypoplastic stomate (arrowed, right). Scale = 100 um. Figure 22. Cuticle from the lower leaf surface of A. sahniana, showing a fully developed stomatal row. Scale = 200 um. Figure 23. Unicellular trichome on the cuticule of A. sahniana. Scale = 10 um. Figure 24. SEM of the inner cuticular surface of A. pancheri, showing a single stomate with granular subsidiary and epidermal cells. x1250.

Figures 25-28. Light micrographs of Acmopyle setiger (lectotype, B-001). Figure 25. Stomatal row from the lower leaf surface containing fully formed stomates. Scale = 100 um. Figure 26. Stomatal row on the upper leaf surface, containing some fully formed stomates and many hypoplastic stomates. Scale = 100 um. Figure 27. A single hypoplastic stomate with the polar and lateral subsidiary cells present, but the guard

mother cell has not divided. Scale = 20 um. Figure 28. Unicellular trichomes at the leaf base. Scale = 20 um. Figures 29-31. Acmopyle florinii (holotype, LB-063). Figure 29. Short shoot, showing bilaterally flattened leaves. Scale = 5 mm. Figure 30. SEM of the inner cuticular surface showing a single stomate. x1185. Figure 31. SEM of the outer leaf surface, showing unicellular trichomes over the midvein. x250.

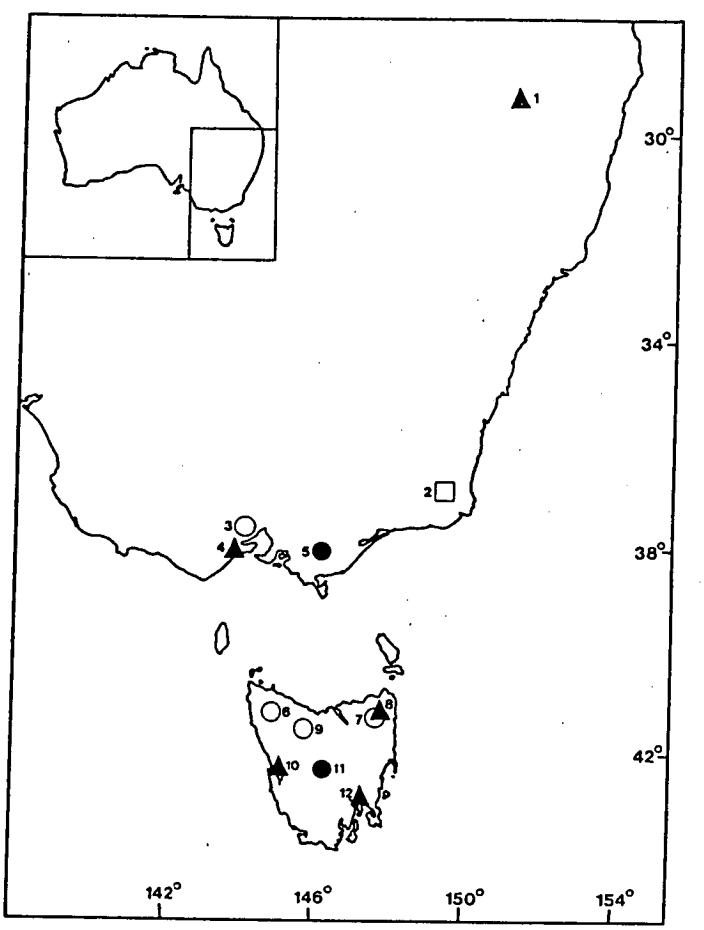
Figures 32-36. Acmopyle glabra (holotype, RPE-006). Figure 32. Short shoot, showing bilaterally flattened leaves. Scale = 5 mm. Figure 33. SEM of a stomatal row on the lower leaf surface. x320. Figure 34. SEM of the inner cuticular surface of the leaf surface containing the fewest stomates. Hypoplastic stomates can be seen in rows. x250. Figure 35. SEM of the inner surface of a hypoplastic stomate, with the polar and lateral subsidiary cells present, although the guard mother cell has not divided. x830. Figure 36. SEM of the inner cuticular surface of the leaf surface containing complete stomatal rows. Two fully formed stomates can be seen. x730. Figures 37,38. Acmopyle glabra from Cethana (C-222). Figure 37. Part of a bilaterally flattened short shoot. Scale = 5 mm. Figure 38. SEM of the inner cuticular surface showing a fully formed stomate. x1200.

Figures 39-41. Acmopyle tasmanica (LA-060, holotype). Figure 39. Light micrograph of cuticle from the upper leaf surface, showing an absence of stomates, either fully formed or hypoplastic. Scale = 100 um. Figure 40. SEM of the inner cuticular surface of the lower leaf surface, showing a single, broad stomatal band. x260. Figure 41. SEM of a single, fully formed stomate from the lower leaf surface. x1000.

Figures 42,43. Counterparts of Podocarpus witherdenensis (holotype, MMF 1201), showing the prominent female cone, and possibly another cone in the early stages of development (arrowed, Fig. 43). Scale = 1 cm. Figure 44. SEM of the inner cuticular surface of P. neriifolius, over a stomatal row, with a vein on the left hand side. x200. Figure 45. SEM of the inner cuticular surface of P. witherdenensis, over a vein. Note the slightly sinuous cell walls. x600. Figure 46. SEM of the inner cuticular surface of P. witherdenensis, over a stomatal row. x1000. Figure 47. SEM of the outer cuticular surface of P. witherdenensis, showing the poorly formed Florin rings. x1000. Figure 48. SEM of the outer cuticular surface of P. neriifolius, showing the poorly formed Florin rings. x800.

Figure 49. History of three imbricate leaved podocarpaceous genera in south-eastern Australia. The solid lines represent the ranges of monophyletic groups. Broken lines repesent less certain phylogenies. The third group in Dacrycarpus represents a large group of species which are not necessarily closely related, but which have similar vegetative structure. There is clear evidence for convergent evolution in response to climatic change in Dacrycarpus.

Figure 50. History of Acmopyle in south-eastern Australia. The solid lines represent the ranges of monophyletic groups. Acmopyle tasmanica is listed as "hypostomatic", but in fact the stomates are restricted to one functional leaf surface which is composed of both adaxial and abaxial sides of the leaf. This is described in more detail in the text. There is clear evidence for convergent evolution in response to climatic change.



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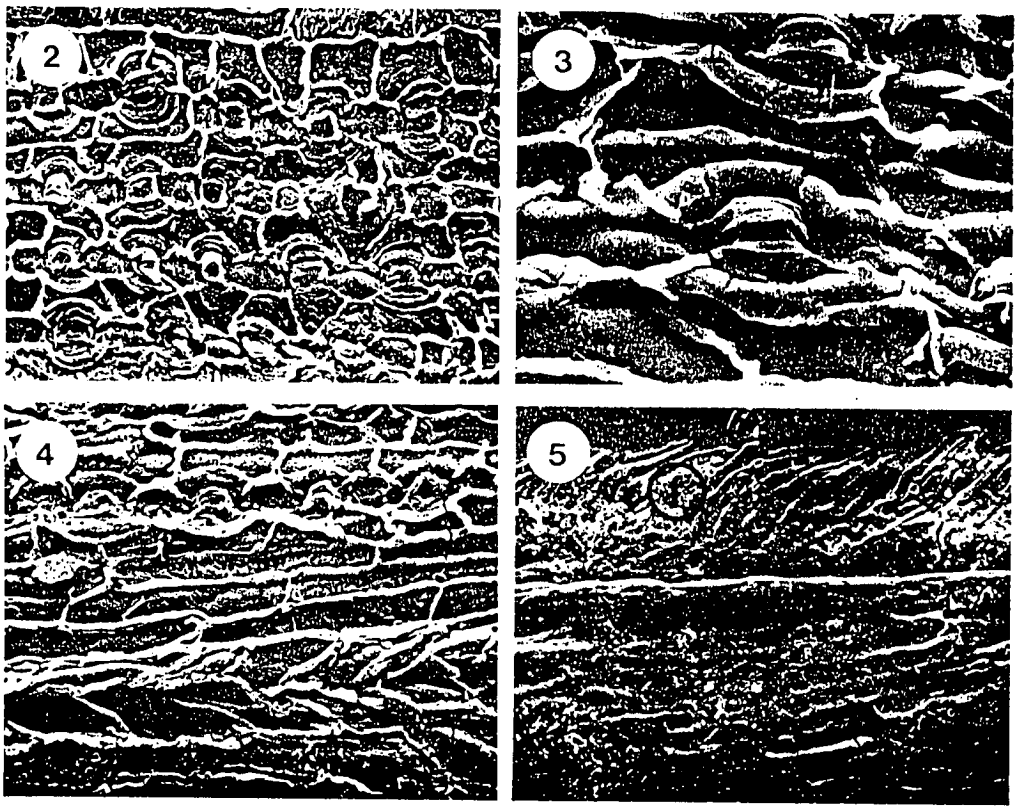
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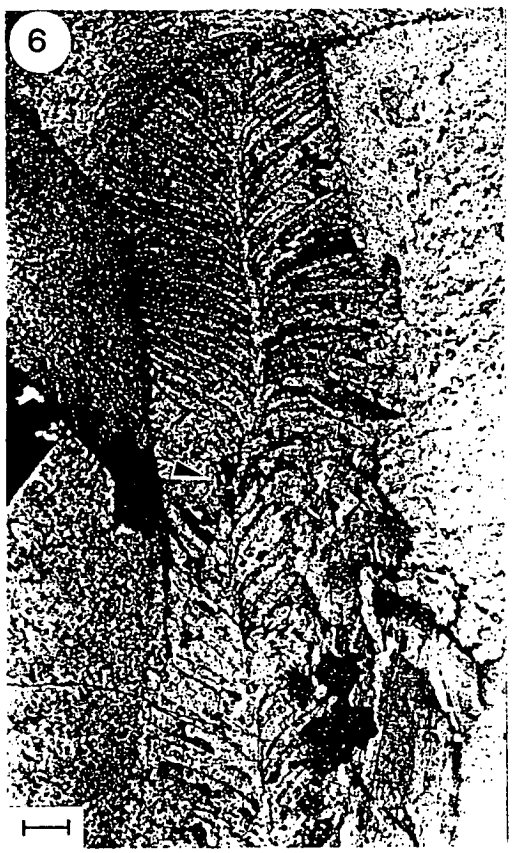
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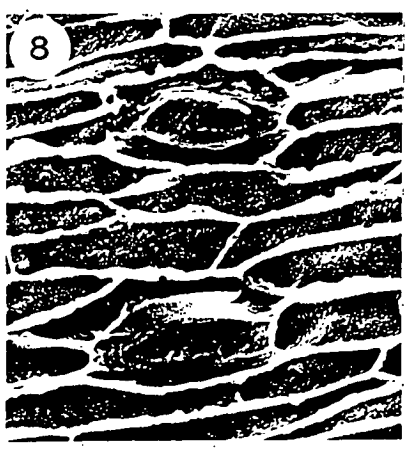
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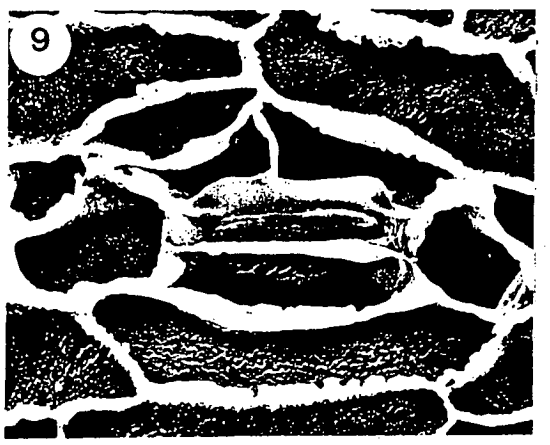
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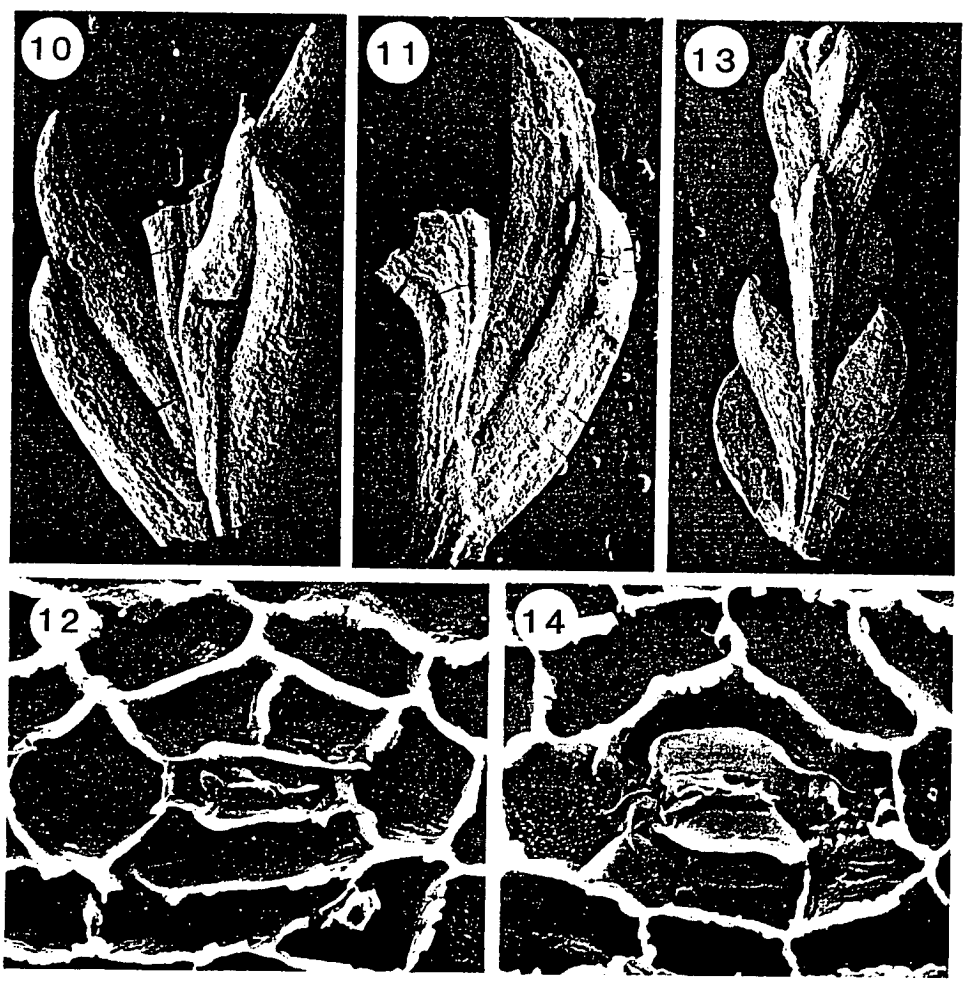
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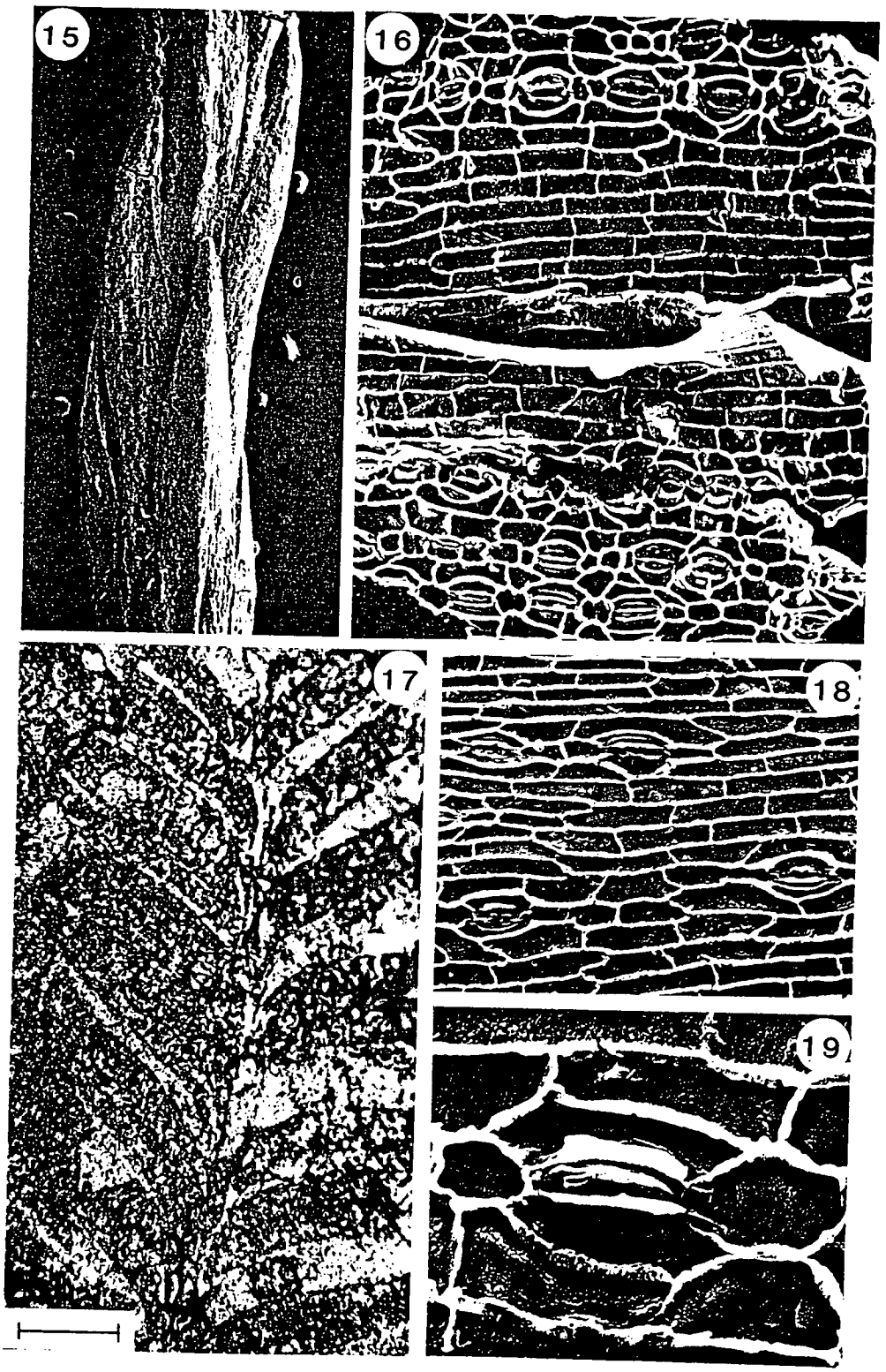
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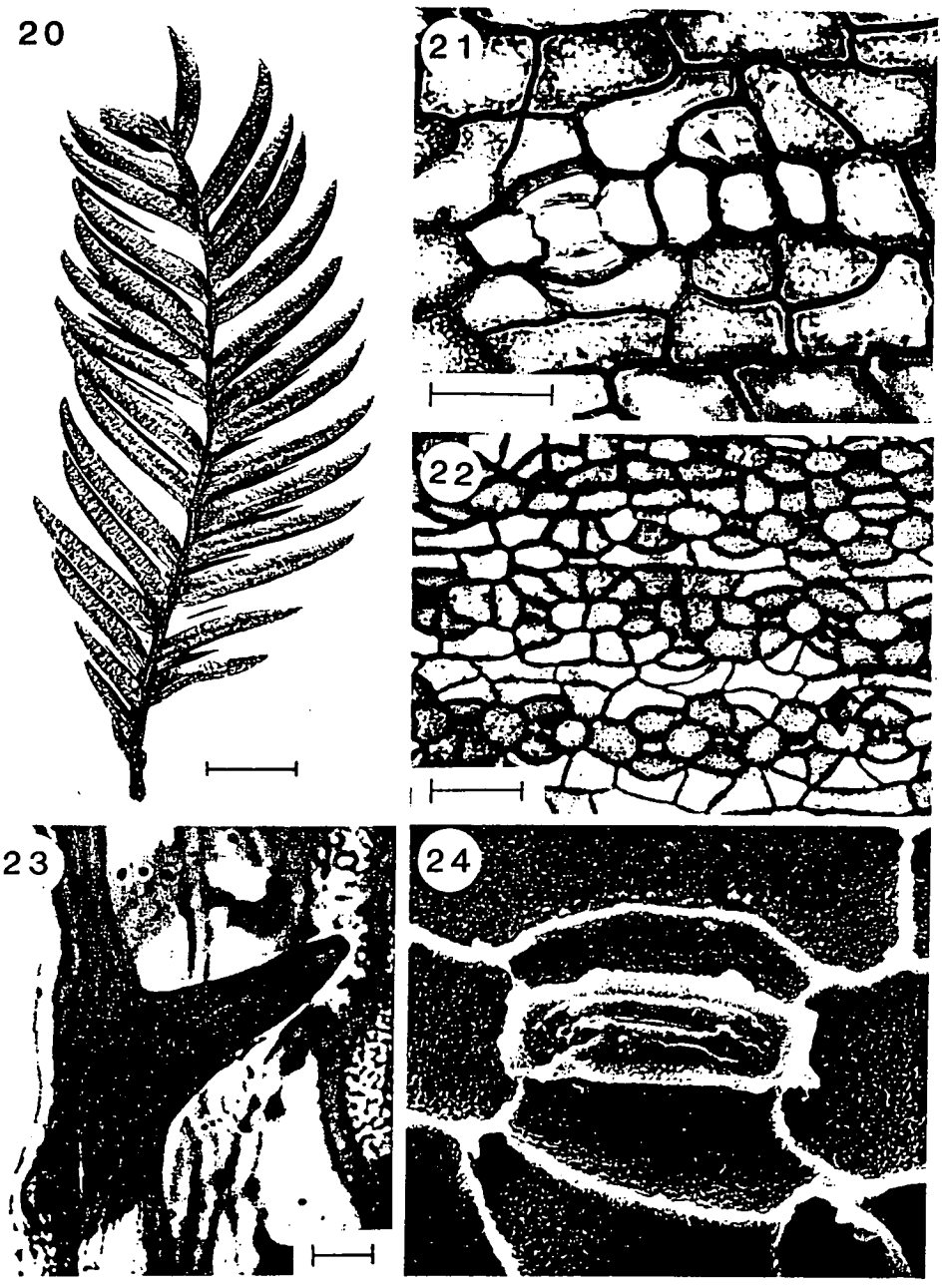
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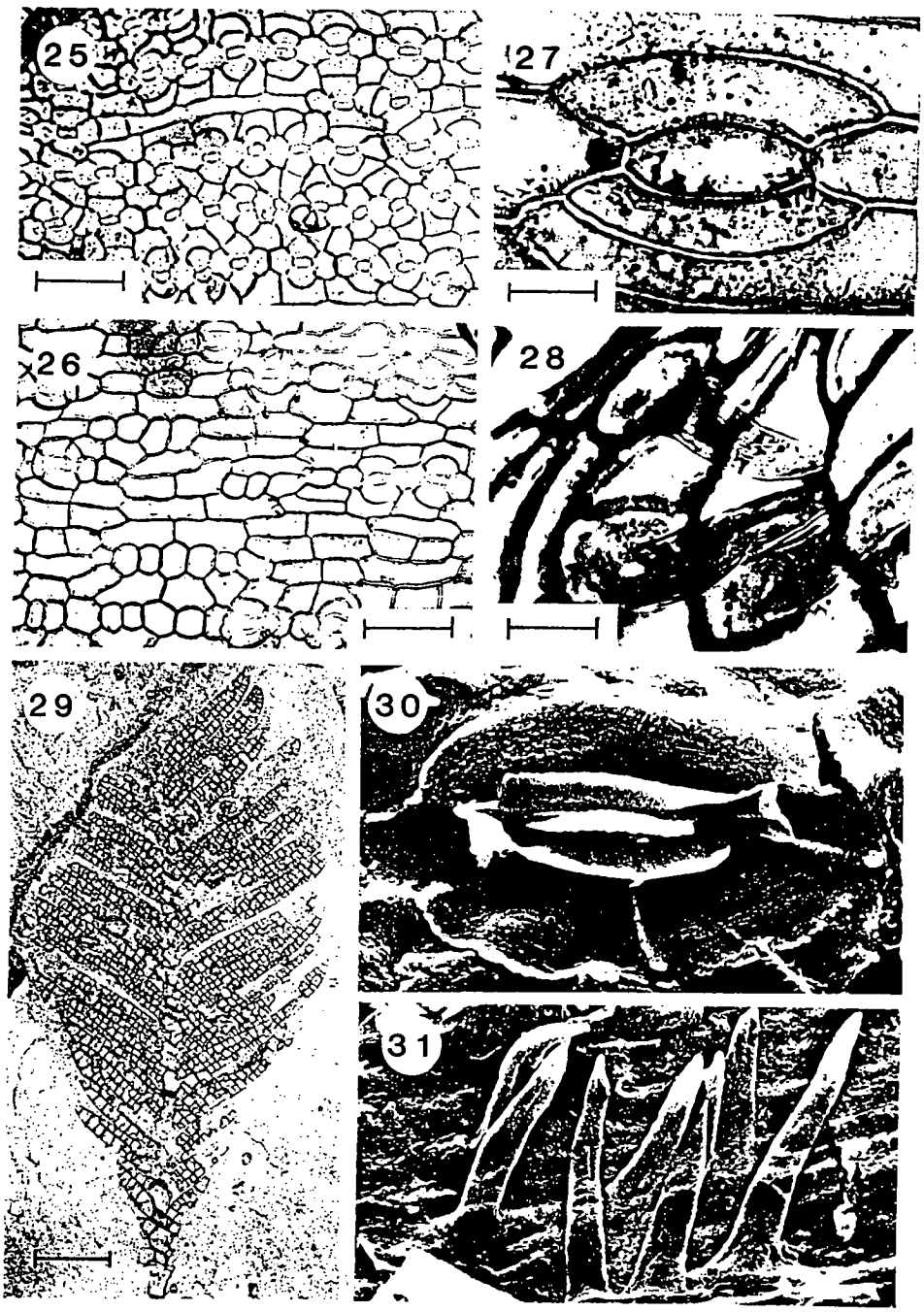
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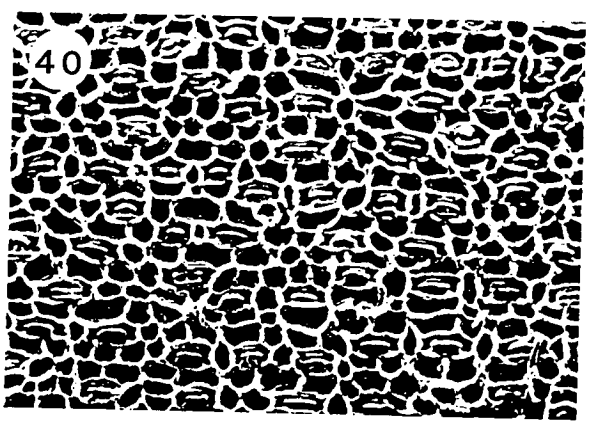
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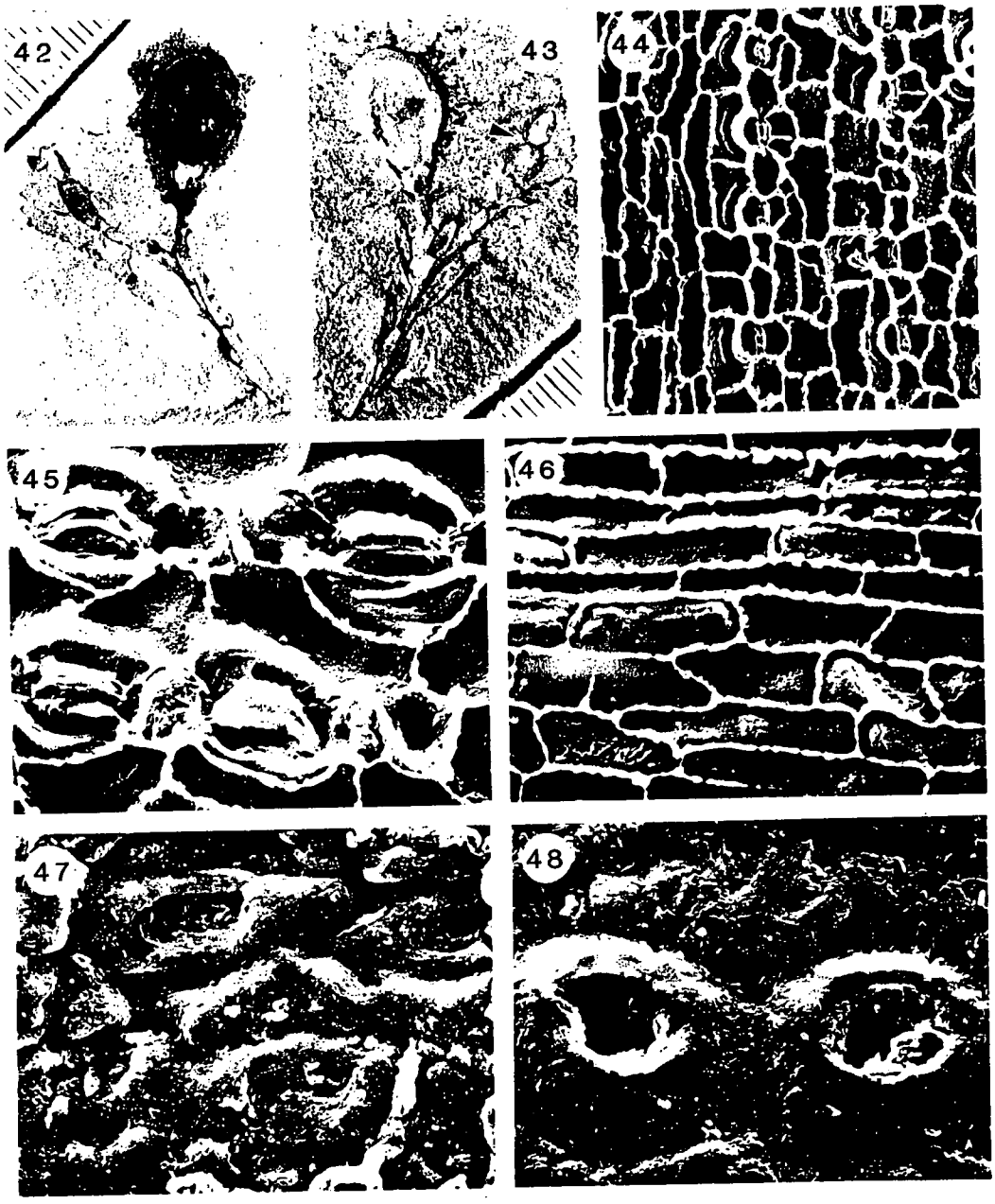
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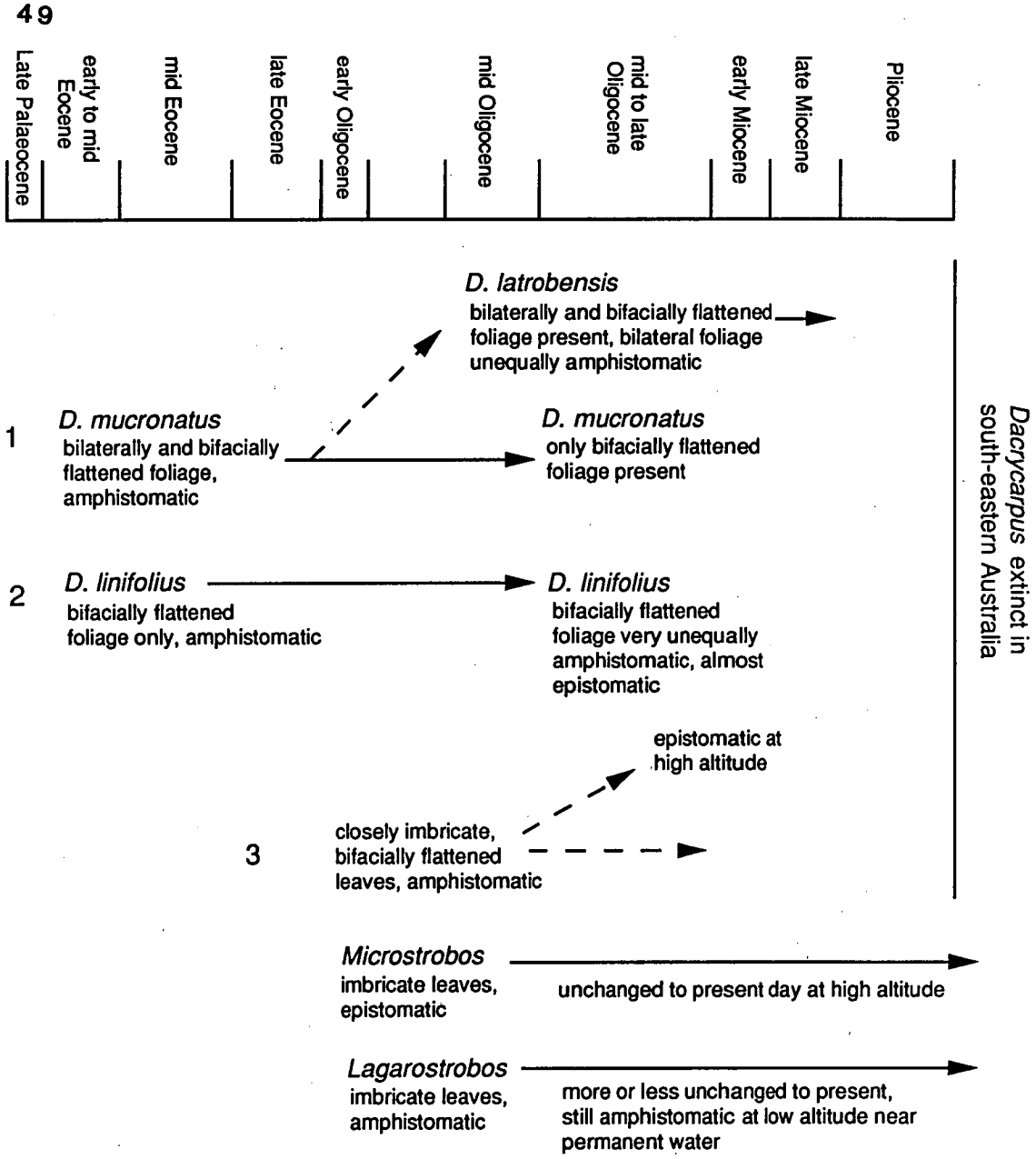
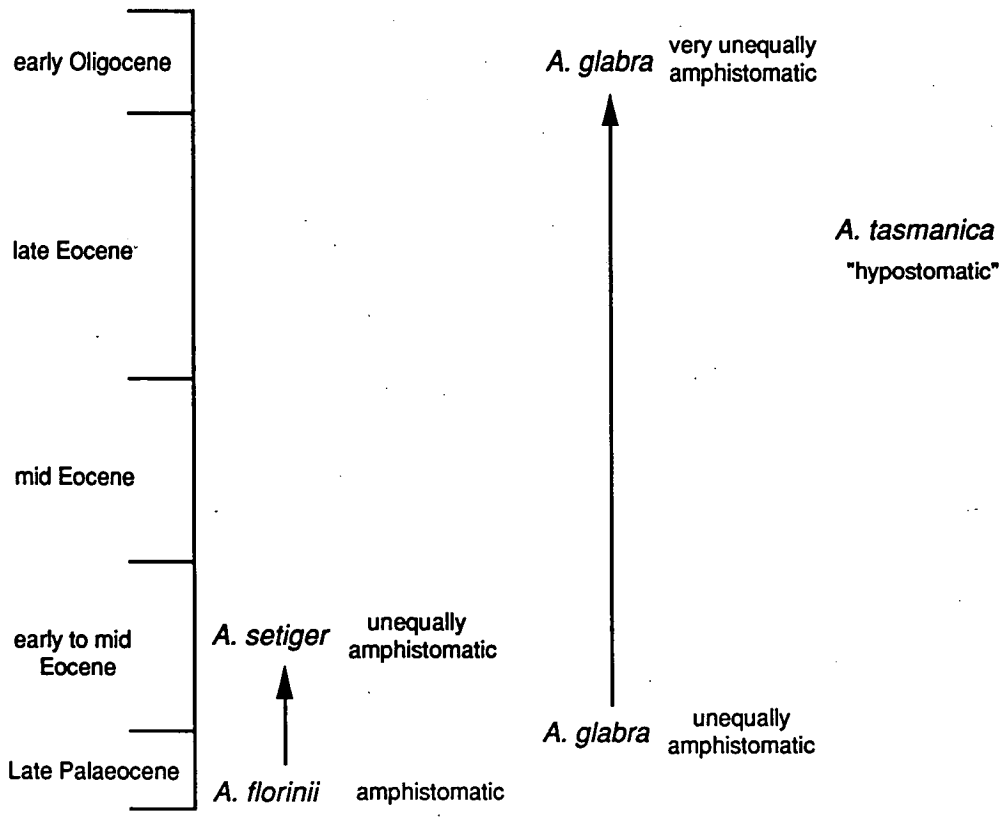

Late Palaeocene
early to mid Eocene
mid Eocene
late Eocene
early Oligocene
mid Oligocene
mid to late Oligocene
early Miocene
late Miocene
Pliocene
D. latrobensis
bilaterally and bifacially flattened foliage present, bilateral foliage unequally amphistomatic
1
D. mucronatus
bilaterally and bifacially flattened foliage, amphistomatic
D. mucronatus
only bifacially flattened foliage present
2
D. linifolius
bifacially flattened foliage only, amphistomatic
D. linifolius
bifacially flattened foliage very unequally amphistomatic, almost epistomatic
epistomatic at high altitude
3
closely imbricate, bifacially flattened leaves, amphistomatic
Dacrycarpus extinct in south-eastern Australia
Microstrobos
imbricate leaves, epistomatic
unchanged to present day at high altitude
Lagarostrobos
imbricate leaves, amphistomatic
more or less unchanged to present, still amphistomatic at low altitude near permanent water


early Oligocene
late Eocene
mid Eocene
early to mid Eocene
Late Palaeocene
A. setiger
unequally amphistomatic
A. florinii
amphistomatic
A. glabra
very unequally amphistomatic
A. glabra
unequally amphistomatic
A. tasmanica
"hypostomatic"

Tertiary gymnosperms from Tasmania: Cupressaceae

ROBERT S. HILL AND RAYMOND J. CARPENTER

HILL, R. S., & CARPENTER, R. J., 1989:03:27. Tertiary gymnosperms from Tasmania: Cupressaceae. *Alcheringa 13*, 89-102. ISSN 0311-5518.

Five new macrofossil species in three genera of the Cupressaceae are described from Oligocene and Miocene deposits in Tasmania. *Papuacedrus australis* is based on vegetative remains from two deposits and cannot be distinguished from the three extant species which are now restricted to New Guinea and the Moluccas. *Libocedrus mesibovii* is based on an ovulate cone, while *L. jacksonii* and *L. morrisonii* are based on vegetative remains. *L. mesibovii* and *L. jacksonii* are found in the same deposit, and may represent different organs of the same species, but this could not be demonstrated. These species clearly belong to *Libocedrus*, which is now restricted to New Zealand and New Caledonia, but are distinct from all extant species considered. *Austrocedrus tasmanica* is based on ovulate cones, and is distinct from the single extant species, which occurs in South America. None of the three genera have been previously reported as fossils outside the range of extant species. The presence of these genera in the Tasmanian Tertiary signals this region as an important centre of diversity for the Cupressaceae at that time.

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Keywords: Tertiary, Tasmania, palaeobotany, macrofossils, gymnosperms, Cupressaceae, *Austrocedrus*, *Libocedrus*, *Papuacedrus*.

THE CUPRESSACEAE are one of the largest conifer families, with 18 genera distributed worldwide. The family can be traced back to the Late Triassic (Miller, 1977), although fossil remains can be difficult to assign to the family because of problems associated with determining the leaf arrangement of compressed specimens. The Cupressaceae are closely related to the Taxodiaceae, and a merger of the two families has been proposed (Eckenwalder, 1976). Miller (1977) supported this merger, although later studies (Miller, 1982) apparently demonstrated a clear distinction between the two. Recently, Hart (1987) concluded that the Cupressaceae form a monophyletic group within the Taxodiaceae, and that a possible solution to the taxonomic problem posed is to merge the two families.

There has been a great deal of debate about the generic limits within the Cupressaceae, and especially within *Libocedrus* (*sensu lato*). This group of 13 species has a complex taxonomic history, summarised by Li (1953a). Today there appears to be little doubt that the three northern hemisphere species belong in a distinct genus, *Calocedrus* (*Heyderia* in many works), which is not closely related to the 10 southern hemisphere species (Li, 1953a; Florin & Boutelje, 1954; Eckenwalder, 1976). However, these remaining 10 species have been variously placed into two genera; *Libocedrus* and *Austrocedrus* (Eckenwalder, 1976), three genera; *Libocedrus*, *Papuacedrus* and *Pilgerodendron* (Li, 1953a), or four genera; *Libocedrus*, *Papuacedrus*, *Austrocedrus* and *Pilgerodendron* (Florin & Boutelje, 1954).

In this study, the four genera of Florin & Boutelje are accepted, and therefore there are currently 11 genera in the subfamily Callitroideae of Li (1953b) given that *Octoclinis* has long been regarded as synonymous with *Callitris*. With the exception of *Tetraclinis*, which Florin (1963) considers on morphological and chemical grounds to be

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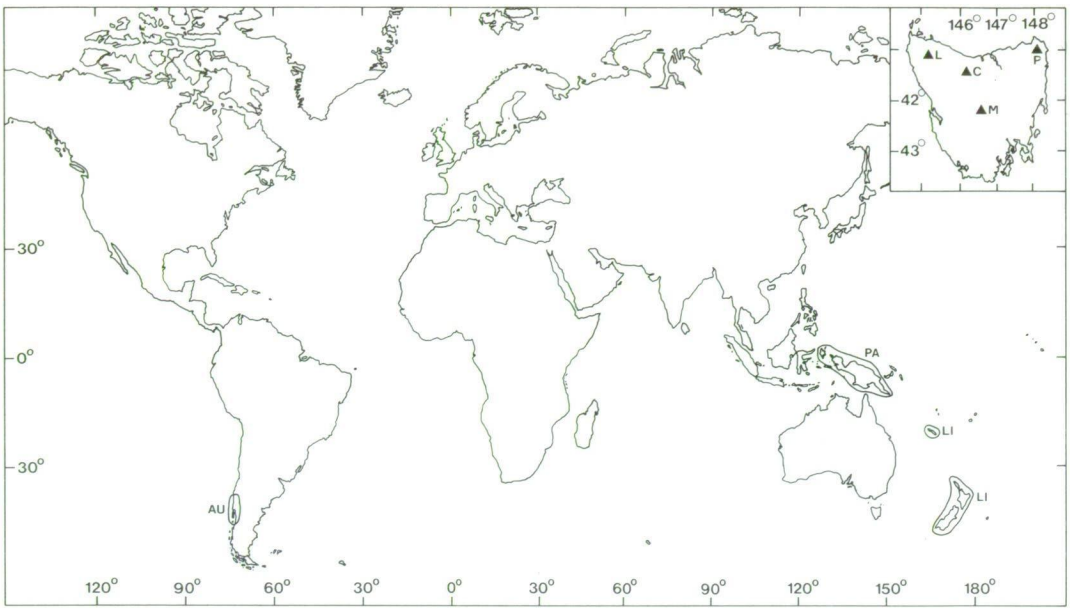


Fig. 1. Map of the world showing the extant distribution of *Austrocedrus* (AU), *Libocedrus* (LI) and *Papuacedrus* (PA). The inset shows the position of the fossil deposits in Tasmania (L = Little Rapid River, C = Cethana, M = Monpeelyata, P = Pioneer).

misplaced in this subfamily, these genera have a southern hemispheric distribution (e.g. Fig. 1). Apart from *Callitris*, all these genera contain five or fewer species and were regarded by Florin (1963) and Miller (1977) as present day remnants of long lines of specialisation. Florin (1963) further noted that most of the genera are confined to the Australasian region. In Australia there are three genera, *Callitris*, which occurs in dry areas, *Actinostrobus*, which is restricted to Western Australia, and *Diselma*, which is restricted to the alpine and subalpine zone of Tasmania.

The fossil record of the Cupressaceae in Australia is sparse. There are few Tertiary pollen records and Martin (1978) notes that the pollen is inconspicuous and relatively uniform, so generic identification is probably not reliable. The macrofossil record (Duigan, 1950) is inconsequential, since none of the reports undertakes even the most basic comparative morphology with extant species. Therefore the discovery of vegetative and reproductive remains from four Tasmanian Tertiary deposits is of major significance in understanding the past distribution of this family and the Tertiary vegetation of south-eastern Australia.

Fossil localities and specimens

The fossils described here are from the following deposits (Fig. 1).

1. Little Rapid River (41 °09 'S., 145 °14 'E.). The fluviatile sands are assigned palynologically to the Lower *Proteacidites tuberculatus* Zone of Stover & Partridge (1973). On this basis and a comparison with other Tasmanian palynofloras, Macphail (*in* Hill, 1987) suggested a Late Oligocene age for the flora. Fossils were retrieved from the sands by maceration in dilute hydrogen peroxide, followed by sieving through a 300 μm sieve. In this way several vegetative fragments and one ovulate cone were retrieved.

2. Pioneer (41 °05 'S., 147 °56 'E.). The fossil-bearing mudstone lenses were considered to be Oligocene on the basis of a palynological examination and the date of overlying basalt (Hill & Macphail, 1983). Several vegetative fragments were retrieved from the mudstone using the technique outlined above.

3. Cethana (41 °32 'S., 146 °07 'E.). The fossil-bearing mudstone was considered on palynological evidence to be of Late Eocene to Oligocene age by Carpenter & Hill (1988). Most fossils are preserved as impressions only, but occasionally organic preservation is found. Several vegetative twigs belonging to the Cupressaceae were recovered.

4. Monpeelyata (42 °40 'S., 146 °04 'E.). Hill & Gibson (1986) reported a probable Late Oligocene or Early Miocene age for this deposit based on an analysis of the microflora and radiometric dates of closely associated basalts. More recently, M. K. Macphail (pers. comm.) has re-analysed the microflora and considers that an Early Miocene age is most likely. Several female cupressaceous cones were retrieved from the mudstone using the technique outlined for Little Rapid River.

Methods

Vegetative twigs from Little Rapid River and Pioneer were cleaned with hydrofluoric acid and mounted directly on aluminium stubs using double-sided adhesive tape. Cuticle was prepared from some fossil specimens by soaking vegetative fragments in 10% chromium trioxide until only the cuticle remained. This cuticle was washed and also mounted on aluminium stubs. Attempts were made to obtain organic remains from the Cethana specimens for similar treatment, but this was unsuccessful. The ovulate cones from Little Rapid River and Monpeelyata were also cleaned in hydrofluoric acid and mounted on aluminium stubs.

Many extant species in the Cupressaceae were available for comparison with the fossils, but the comparison was restricted to those with a similar leaf arrangement or species with a southern hemispheric distribution (Table 1). Vegetative twigs and cuticle of these extant species were soaked in chloroform to remove leaf waxes and attached to aluminium stubs for study with the scanning electron microscope. Ovulate cones of some species were also attached to stubs but without any prior preparation. The specimens on aluminium stubs were gold-coated in a high vacuum evaporative coating unit to a maximum thickness of 20 nm. Specimens were then studied using a Philips 505 scanning electron microscope operated at 15 kV. Ovulate cones of some extant species which were too large to photograph with the scanning electron microscope were photographed with reflected light.

Species	Geographic locality
Austrocedrus chilensis	South America
Callitris columnaris	Australia
C. oblonga	Tasmania
C. preissii	Australia
C. rhomboidea	Australia
Calocedrus decurrens	Northern hemisphere
C. formosana	Northern hemisphere
Chamaecyparis lawsoniana	Northern hemisphere
C. nootkatensis	Northern hemisphere
Diselma archeri	Tasmania
Fitzroya cupressoides	South America
Fokienia hodginsii	Northern hemisphere
Libocedrus austro-caledonica	New Caledonia
L. bidwillii	New Zealand
L. plumosa	New Zealand
Papuacedrus arfakensis	New Guinea, Moluccas
P. papuana	New Guinea
P. torricellensis	New Guinea
Pilgerodendron uviferum	South America
Thuja occidentalis	Northern hemisphere
T. plicata var. *zedrina*	Northern hemisphere
T. standishii	Northern hemisphere
Thujopsis dolabrata	Northern hemisphere

Table 1. List of extant species in the Cupressaceae which were available for comparison with the fossils, along with their current geographic range.

Comparison of fossil and living species

Ovulate cones

The fossil ovulate cone from Little Rapid River (Fig. 2A, B) has four valvate cone scales, three long and one about half the length. At the base of two long cone scales are leaf-like structures (Fig. 2A, B) which are absent from the other cone scales. There is no sign of any appendages on the cone scales except at the apex, where there is evidence of an appendage on at least two and possibly all three visible scales (Fig. 2A). This apical appendage is missing and so its morphology and size is unknown. The cone is subtended by several opposite pairs of scale leaves (Fig. 2B). One of these scale leaves was removed for further examination, but no cuticular details could be determined.

This cone type is similar to that described by Li (1953a) for *Libocedrus*. In particular, the feature that separates *Libocedrus* from the closely related *Papuacedrus* and *Austrocedrus* is the presence in the former of a short or long, more or less sharp spine or a bract on the abaxial surface of the ovuliferous scales (de Laubenfels, 1972; Salmon, 1980). This spine may arise anywhere in the apical half ot the scale. In comparison, *Papuacedrus* has a large, triangular or ovate appendage on the abaxial surface of the ovuliferous scales near the base or below the centre (Fig. 2C), and *Austrocedrus* ovuliferous scales are each furnished with a minute 'tubercle' on the abaxial surface just below the apex (Florin & Boutelje, 1954, Fig. 2D). Therefore, the cone from Little Rapid River fits the description of *Libocedrus* and is distinct from the other related genera.

The ovulate cones from Monpeelyata are distinct from the Little Rapid River specimen (Fig. 2E, F compared with Fig. 2A), but are very similar to those of *Austrocedrus chilensis*

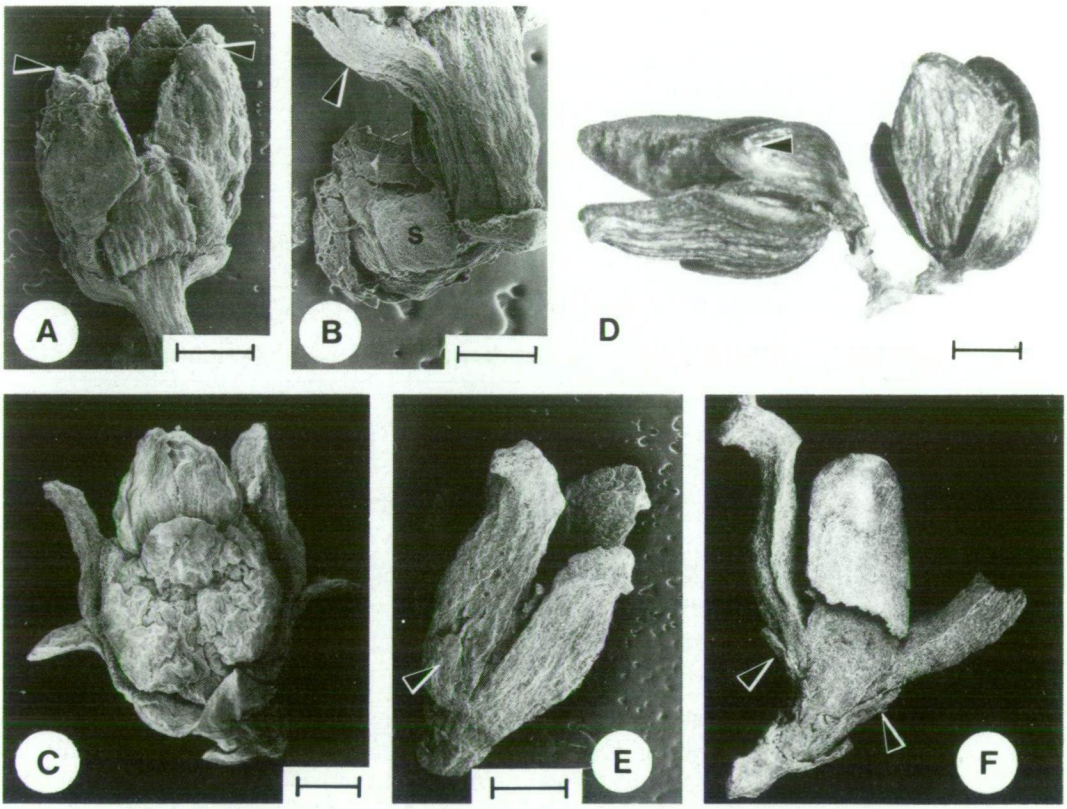


Fig. 2. A, Ovulate cone of *Libocedrus mesibovii* (type specimen, LRR1-879). Note the three large cone scales (one on each side, one at the rear), and the fourth, smaller cone scale at the front. The imbricate leaf-like structures at the base of the two large cone scales on the sides can be seen, and the arrows indicate the position of attachment of appendages. There may also be a scar on the third visible scale, but this is less certain. Scale = 1 mm. B, Base of the cone shown in Fig. 2A. Note the imbricate scale leaves (one marked s) which are arranged in opposite pairs, and the arrowed leaf-like structure which subtends one of the large cone scales. Scale = 0.5 mm. C, Ovulate cone of *Papuacedrus papuana*. Note the bract-like appendages which arise from each cone scale about halfway up. Scale = 1 mm. D, Ovulate cones of *Austrocedrus chilensis*. Note the valvate arrangement of the cone scales and the tubercles (arrowed on two scales) which occur near the apex of each cone scale. Scale = 2.5 mm. E, Ovulate cone of *Austrocedrus tasmanica* (M-1942, type specimen). Note the valvate arrangement of the cone scales and the prominent tubercle near the apex of each cone scale. An imbricate leaf-like structure at the base of one of the large cone scales is arrowed. Scale = 1 mm. F, Ovulate cone of *A. tasmanica* (M-1938). Note the imbricate leaf-like structure at the base of the two large cone scales (arrowed) and the remains of oppositely arranged leaves below them. Scale as for 2E.

(Fig. 2D), the only extant species in the genus. In particular, they possess the minute 'tubercles' on the abaxial surface of each ovuliferous scale (Fig. 2D, E) which Florin & Boutelje (1954) considered were diagnostic of the genus. Therefore, these cones can be placed in *Austrocedrus* with confidence.

Vegetative remains

Three types of vegetative remains have been recovered (Figs 3A-D, 5A-E), and all have flattened branches with opposite pairs of facial and lateral leaves which is characteristic of the Cupressaceae. The leaf arrangement of the Cupressaceae basically falls into one of three types: whorls of three, whorls of four, or opposite pairs (Figs 3E-I, 5F, G). The fossils from Little Rapid River and one of the species from Pioneer (Fig. 3A-D) have opposite pairs of leaves on a flattened branch system. This arrangement is found in *Austrocedrus* (Fig. 3E), *Chamaecyparis* (Fig. 3G) and *Libocedrus* (Fig. 3H, I). *Papuacedrus* is usually regarded as having this leaf arrangement, but the leaves are fused (Friis, 1977) whereas those in the fossils are free. The leaf arrangement of *Papuacedrus* will be considered in more detail later. *Austrocedrus* leaves have indistinct margins (Florin & Boutelje, 1954, Fig. 3E), which is not the case in either of the fossil types. Therefore, the fossils are most similar to *Chamaecyparis* and

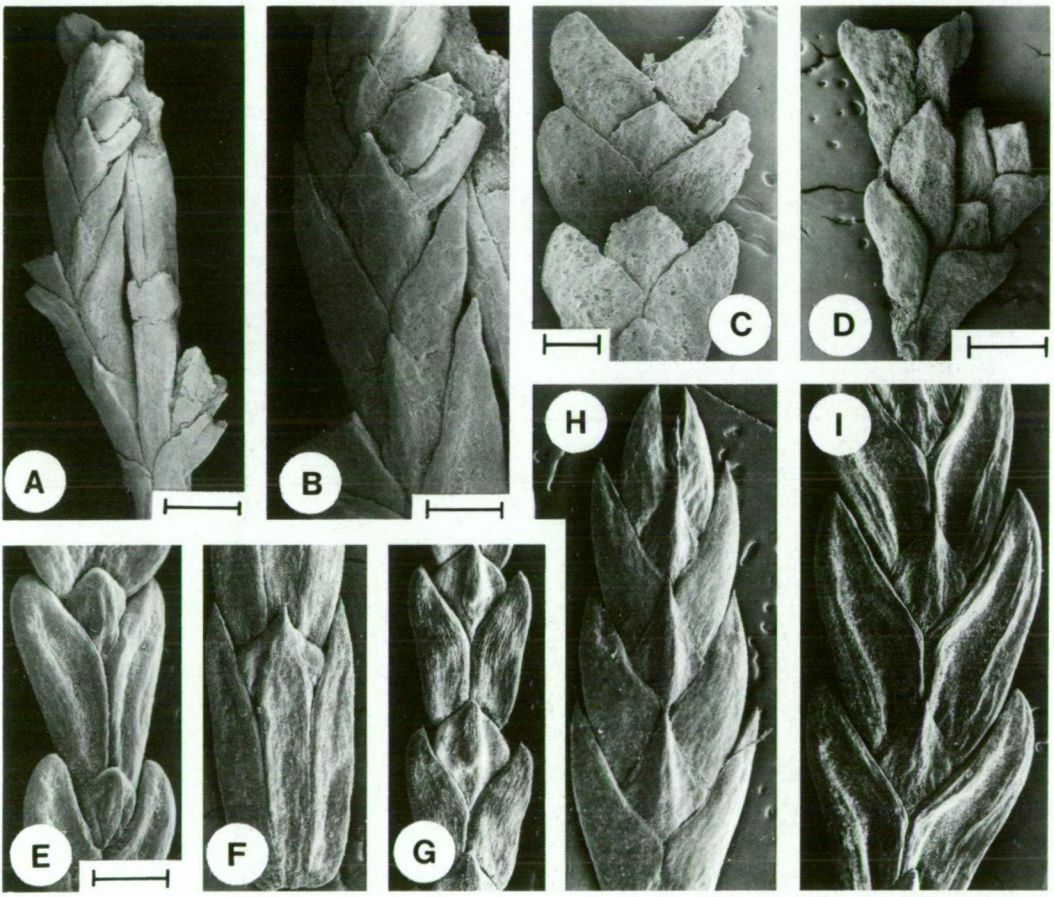


Fig. 3. Scanning electron micrographs of fossil and extant leaf-bearing branches. A, B, *Libocedrus morrisonii* (P-343, type specimen). Scale for A = 1 mm, B = 0.5 mm. C, *L. jacksonii* (LRR1-880, type specimen). Scale = 0.5 mm. D, *L. jacksonii* (LRR1-1264). Scale = 0.5 mm. E, *Austrocedrus chilensis*. The leaves are arranged in opposite pairs. Scale = 1 mm. F, *Calocedrus decurrens*. The leaves are arranged in whorls of four. Scale as for E. G, *Chamaecyparis lawsoniana*. The leaves are arranged in opposite pairs. Scale as for E. H, *Libocedrus austro-caledonica*. The leaves are arranged in opposite pairs. Scale as for E. I, *L. plumosa*. The leaves are arranged in opposite pairs. Scale as for E.

Libocedrus. These two genera are difficult to separate vegetatively, although they are not closely related. Cuticle is preserved on both fossil types (Fig. 4A, B, E, F), but this does not assist in determining the generic identity of the fossils. We consider it possible that the foliage at Little Rapid River is conspecific with the *Libocedrus* ovulate cone (Fig. 2A, B), although there is no organic connection. The presence of this cone, along with the current restriction of *Chamaecyparis* to the northern hemisphere and the presence of *Libocedrus* today in New Zealand and New Caledonia (Fig. 1) prompts us to place the fossils in *Libocedrus* rather than erect a form genus.

The second fossil type from Pioneer (Fig. 5C-E) is very similar in leaf arrangement to the fossils from Cethana (Fig. 5A, B). In the absence of organic preservation in the Cethana fossils it is impossible to separate them from the Pioneer specimens and they must be considered as conspecific. The fossils are indistinguishable from *Papuacedrus*, and this is highlighted by three distinctive features. Firstly, the lateral leaves on the flattened branches are substantially larger than the much reduced facial leaves (Fig. 5F, G). Secondly, while *Papuacedrus* is usually reported as having opposite pairs of leaves, all three extant species appear to have the leaves in whorls of four, although the attachment of the facial leaves is very narrow, making it appear as though the decurrent bases of the lateral leaves join together (Fig. 5G). Thirdly, the leaves fuse towards the base in *Papuacedrus* (Fig. 5G). All these features can clearly be seen in the fossils (Fig. 5A-E) and allow them to be assigned to *Papuacedrus* with confidence.

Systematics

Family CUPRESSACEAE

Austrocedrus Florin & Boutelje 1954

A. tasmanica sp. nov. (Fig. 2E, F)

Diagnosis. Ovulate cone with four valvate scales in two pairs of differing size, with the smaller pair being about 75% as long as the larger pair. Large scales about 4 mm long, 1-1.5 mm wide. Each scale bears a tubercle abaxially just below the apex, which is about 0.5 mm long and about 0.5 mm wide. The large scales are subtended by imbricate leaves and below that by opposite pairs of leaves in a three dimensional arrangement.

Holotype. M-1942 (Fig. 2E), stored in the palaeobotany collection, Department of Plant Science, University of Tasmania.

Type locality. Monpeelyata, central Tasmania (Early Miocene).

Specimens examined. M-118, M-1938, M-1941, M-1942, M-1943.

Etymology. The specific epithet refers to the distribution of the species, being the first record of the genus outside South America.

Discussion. The cones of *A. tasmanica* (Fig. 2E, F) differ from those of *A. chilensis* (Fig. 2D), the only extant species in the genus, in three main respects. Firstly, the fossil cones are substantially smaller, although this should not be treated as an important taxonomic character in isolation. Secondly, the smaller pair of scales in *A. tasmanica* are generally about 75% of the length of the larger pair of scales, whereas in *A. chilensis* they rarely exceed 50% (Fig. 2D-F). Thirdly, the larger pair of scales in *A. tasmanica* are subtended by a relatively large pair of leaves which overlap the scales substantially (Fig. 2E, F). These leaves do not occur in *A. chilensis*. Thus, *A. tasmanica* is clearly distinct from *A. chilensis*. Unfortunately, despite an intensive search, no recognisably cupressaceous foliage has been recovered from Monpeelyata. Berry (1938) described *Libocedrus prechilensis* from the Miocene of Argentina and considered that it closely resembled *L. chilensis* (now *Austrocedrus chilensis*). However, Berry's fossil was entirely vegetative, and so no comparison can be made with *A. tasmanica*.

Libocedrus Endlicher 1847

L. mesibovii sp. nov. (Fig. 2A, B)

Diagnosis. Ovulate cone with four valvate scales in two pairs. One pair of scales relatively long and wide, the other pair

unequal in size, one as long as the larger valves but narrower, the other about half as long and narrower. Large scales about 3.5 mm long and about 3 mm wide. Each of the larger scales with a scar near the apex where a spine was borne. Imbricate leaf-like structures opposite one another at the base of two large scales. Imbricate leaves in opposite pairs below the cone.

Holotype. LRR1-879 (fig. 2A, B), stored in the palaeobotany collection, Department of Plant Science, University of Tasmania.

Type locality. Little Rapid River, north-western Tasmania (Late Oligocene).

Specimen examined. LRR1-879.

Etymology. Named for Mr Bob Mesibov, who first made us aware of the deposit and showed a keen interest in assisting in its preservation.

Discussion. The single ovulate cone of *L. mesibovii* (Fig. 2A) may not be typical of the species in that it contains the typical larger pair of scales, but the smaller pair are not of equal size which is the usual situation in extant *Libocedrus*. Unfortunately, the spines or bracts on the abaxial surface of the scales are not preserved, so no comparison can be made. However, the attachment is near the apex, and is small and somewhat circular (Fig. 2A). The New Zealand species have a broad attachment of the bract-like structure, further away from the apex, quite unlike the fossil, whereas the New Caledonian species have a spine-like structure which arises near the apex. On this basis the similarity is with the New Caledonian species. At the base of the cone are an opposite pair of leaf-like structures (Fig. 2A, B), at the base of two of the large scales. While similar structures have been seen on illustrations of extant *Libocedrus* cones, the fossil cone appears to be unusual in having a pedicel which is not covered in leaves below these leaf-like structures (Fig. 2B).

L. jacksonii sp. nov. (Figs 3C, D, 4A, B)

Diagnosis. Branches flattened, with opposite pairs of lateral and facial leaves. Facial leaves up to 1 mm long, length:width ratio slightly greater than 1, the free portion with convex margins, slightly keeled, apex bluntly acute. Lateral leaves not fused to facial leaves, with a strongly developed margin, up to 2 mm long and up to 1 mm wide, about equal projection with facial leaves. Lateral leaf margin well developed, convex, or concave at the midpoint, and convex at the apex, apex bluntly acute. Stomatal distribution unknown. External stomatal opening with a pronounced Florin ring with a high ridge, up to six lobes, and with a peripheral groove. Well developed circular papillae common between stomata. Inner surface of stoma typically cupressaceous, indentations for papillae not conspicuous.

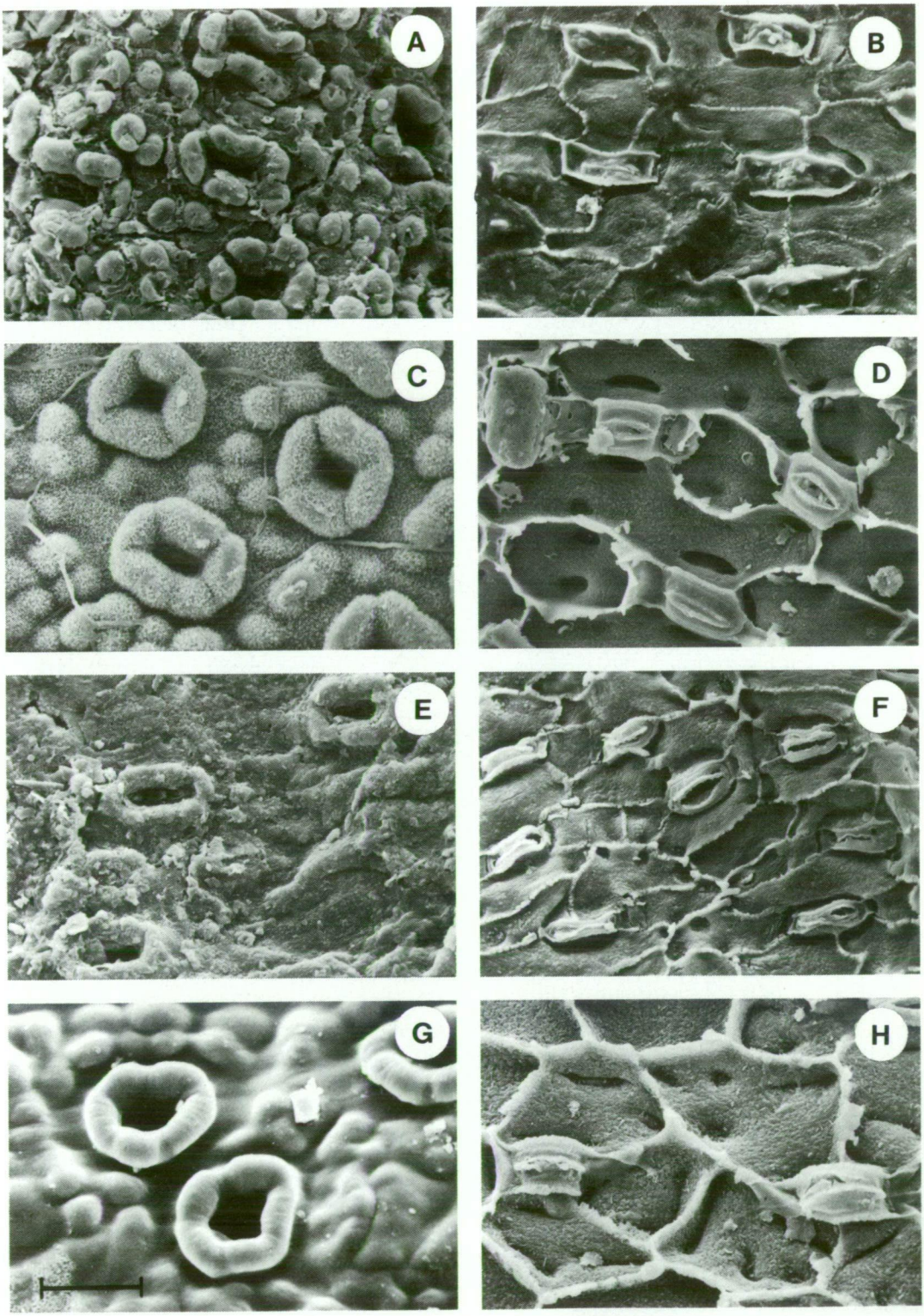
Holotype. LRR1-880, stored in the palaeobotany collection, Department of Plant Science, University of Tasmania.

Type locality. Little Rapid River, north-western Tasmania (Late Oligocene).

Specimens examined. LRR1-880, LRR1-1264 to 1270.

Etymology. Named for Prof. W. D. Jackson, on his retirement from the Botany Department, University of Tasmania, and in recognition of his unique understanding of the extant Tasmanian vegetation.

Discussion. Vegetative specimens of three of the five extant *Libocedrus* species were available for comparison with the fossils (Table 1), and illustrations of the other two were helpful. The branches of *L. jacksonii* are distinctly flattened, and the leaves appear to be more truncated than any of the extant species (Fig. 3C, D). The stomatal morphology of the Cupressaceae is variable (Oladele, 1983a, b), although the main variability is among genera rather than within them. The external cuticular pattern of *L. jacksonii* is very similar to that of *L. austrocaledonica* in the form of the Florin rings and the numerous circular papillae between the stomata (Fig. 4A, C). However, *L. austrocaledonica* exhibits deep indentations on the inner surface where the papillae arise, and these are not apparent in *L. jacksonii* (Fig. 4B, D). The fossil is clearly distinct from all extant species observed. The only previously published record of *Libocedrus* in the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southern hemisphere is the report by Couper & McQueen (1954) of foliage of *L. plumosa* from the Upper Miocene-Pliocene Great Barrier Island. Although the foliage was not illustrated, the fact that it is assigned to an extant species suggests that it is distinct from the fossil species reported here.

It is possible that the ovulate cone (*L. mesibovii*) and the foliage (*L. jacksonii*) represent different organs of the same species. Attempts were made to obtain cuticle from the imbricate leaves of *L. mesibovii* for comparison with *L. jacksonii*, but this failed. There are situations today where more than one species of *Libocedrus* occur together and in the absence of proof to the contrary, these specimens must be considered as distinct species.

L. morrisonii sp. nov. (Figs 3A, B, 4E, F)

Diagnosis. Branches partially flattened, with opposite pairs of lateral and facial leaves. Facial leaves up to 1.5 mm long and up to 0.7 mm wide, the free portion about the same size and shape as the visible attached portion. Leaf apex acute, apical portion slightly keeled. Lateral leaves not fused to facial leaves, with a strongly developed margin, up to 2.5 mm long and up to 0.6 mm wide. Lateral leaves less than, equal to, or above the facial leaves, apex acute. Stomatal distribution unknown. External stomatal opening with a pronounced Florin ring with a high ridge, about four lobes and without a peripheral groove. Papillae not observed. Inner surface of stomata typically cupressaceous, occasional indentations on epidermal cells may indicate presence of papillae on outer surface.

Holotype. P-343 (Fig. 3A, B), stored in the palaeobotany collection, Department of Plant Science, University of Tasmania.

Type locality. Pioneer, northeastern Tasmania (Oligocene).

Specimens examined. P-343, P-661 to P-667, P-921 to P-924, P-1152.

Etymology. The species is named for Mr Ken Morrison, who first brought the deposit to the attention of the first author.

Discussion. There is little variation in leaf size and shape among specimens of *L. morrisonii.* The branches are slightly flattenend, but of all the fossils examined, these retain most evidence of three dimensional structure (Fig. 3A, B). There is a great deal of similarity in leaf morphology and arrangement between *L. morrisonii* and all extant species. This similarity extends to both lateral and facial leaf size, shape and arrangement. It is also notable that the facial leaves of *L. morrisonii* are keeled towards the apex, a feature which is clear in the extant species (Fig. 3A, B, H, I).

The distribution of stomata on the fossils is unknown, since the cuticle is poorly preserved and could only be described from fragments. Attempts to observe stomata on whole shoots under the scanning electron microscope were unsuccessful. The external Florin ring morphology of *L. morrisonii* is similar to all extant *Libocedrus* species observed (Fig. 4C, E, G), as is the internal stomatal morphology (Fig. 4D, F, H). One of the more unusual features of *L. morrisonii* is the lack of well developed papillae between the stomata (Fig. 4E), but a similar poor development was observed on *L. plumosa* (Fig. 4G). No extant or fossil species was found that matched *L. morrisonii* in all aspects, and this, along with the age of the fossil and its geographic isolation, prompted the erection of a new species.

Papuacedrus Li 1953a

P. australis sp. nov. (Figs 5A-E, 6A, B)

Diagnosis. Branchlets flattened, with leaves in whorls of four. Leaf whorls up to 8 mm

Fig. 4. Scanning electron micrographs of cuticles of living and fossil species. Scale = 25 μm. A, *Libocedrus jacksonii*, outer surface (LRR1-880). Note the lobed Florin rings and the papillae between them. B, *L. jacksonii*, inner surface (LRR1-1265). C, *L. austro-caledonica*, outer surface. The wax crystals remain on this specimen, but they do not obscure the lobed Florin rings and the papillae between them. D, *L. austro-caledonica*, inner surface. E, *L. morrisonii*, outer surface (P-662). Note the weakly lobed Florin rings and the absence of papillae. F, *L. morrisonii*, inner surface (P-662). G, *L. plumosa*, outer surface. Note the weakly lobed Florin rings and poorly developed papillae between them. H, *L. plumosa*, inner surface.

long and up to 5 mm wide. Facial leaves with long, narrow attachment, probably fused to the lateral leaves. Free portion of facial leaves smaller than lateral leaves or reduced and scale-like, apex acute. Lateral leaves with strongly developed leaf margin, variable shape, apex acute. Stomata restricted to one leaf surface. External stomatal opening with a pronounced Florin ring with a high ridge, lobing poorly developed and no peripheral groove. Papillae poorly developed or absent. Inner surface of stomata typically cupressaceous.

Holotype. P-1168 (Fig. 5E), housed in the palaeobotany collection, Department of Plant Science, University of Tasmania.

Type locality. Pioneer, northeast Tasmania (Oligocene). There is an additional occurrence at Cethana, northern Tasmania (Late Eocene-Oligocene).

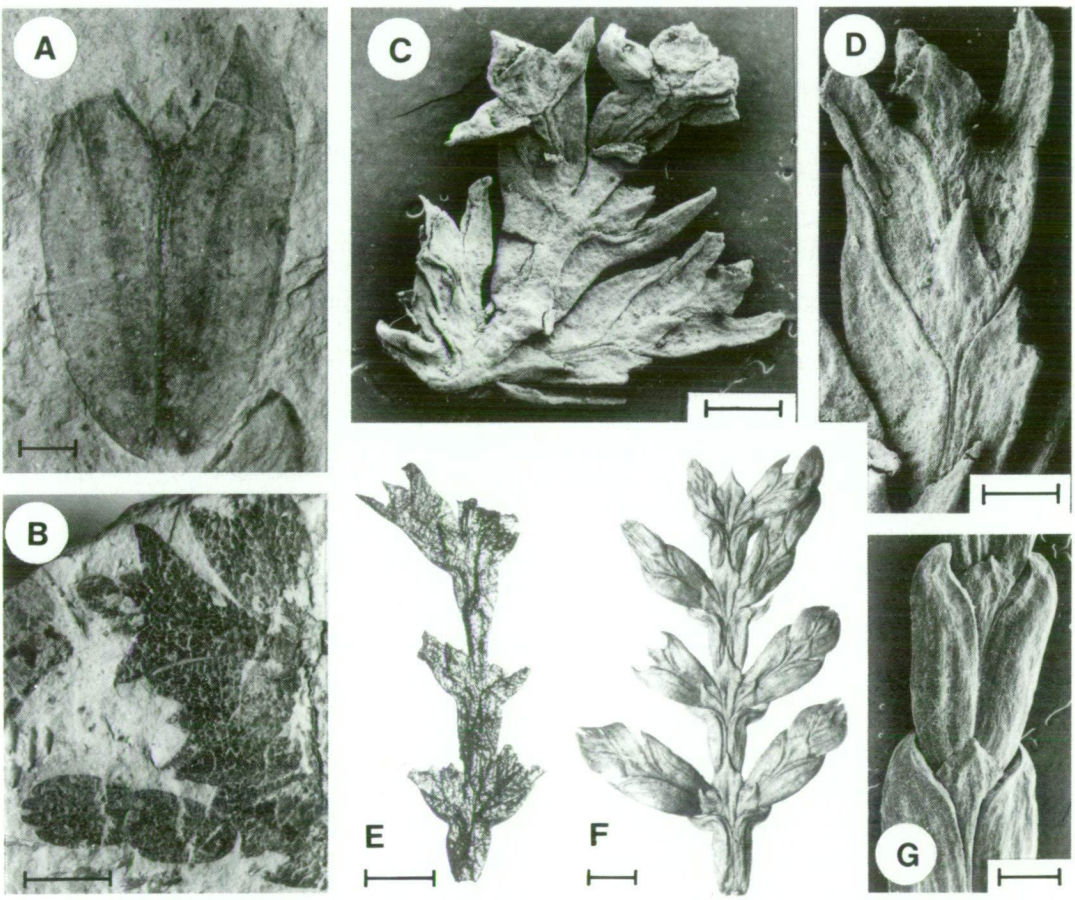

Fig. 5. A, *Papuacedrus australis* from Cethana (C-225). the fossil consists of a single leaf whorl. Note the relatively small size of the facial leaf. Scale = 1 mm. B, *P. australis* from Cethana (C-234). The fossil consists of leaf-bearing branches, but detail is not well preserved. Scale = 2 mm. C, Scanning electron micrograph (SEM) of a leaf-bearing branch of *P. australis* from Pioneer (P-1166). Scale = 1 mm. D, Enlargement of part of 5C. Note that the lateral leaves fuse to the facial leaf, and the leaf arrangement is whorls of four. The facial leaf is relatively large compared with that in 5A. Scale = 0.5 mm. E, *P. australis* from Pioneer (P-1168, type specimen). Note the leaf arrangement and branching pattern. Scale = 2 mm. F, *P. papuanus*. Note the leaf arrangement and branching pattern compared with 5E. Scale = 2 mm. G, SEM of a leaf-bearing branch of *P. papuanus*. Note that the lateral leaves fuse with the facial leaf, and the leaf arrangement is whorls of four. Scale = 1 mm.

Specimens examined. P-1166-1170, C-225, C-234, C-259, C-349.

Etymology. Named for the southerly occurrence of the fossils, more than 41° S today, approximately 55° S at the time of deposition, compared with the current equatorial distribution of the genus.

Discussion. The specimens of *P. australis* exhibit a range of foliage size and shape (Fig. 5A-E). Two of the specimens from Cethana (e.g. 5A) are isolated leaf whorls which have separated from one another. This probably represents a stage in the decay of the branches. The third specimen from Cethana appears to represent part of a branch tip which is not fully expanded (Fig. 5B). The foliage from Pioneer is variable in size and shape, and includes the Cethana specimens in its range, although the lateral leaves of the Cethana specimens are generally larger and the facial leaves smaller (Fig. 5A compared with Fig. 5D). The mature foliage of the three extant species of *Papuacedrus* is extremely variable in morphology, and examples can be found in each which closely match the fossils (Fig. 5G). Therefore, it is impossible to determine which extant species the fossils are most closely related to based on leaf morphology alone. Similarly, the cuticular pattern of the Pioneer specimens matches very well with the extant *Papuacedrus* species (Fig. 6A-D), but it cannot be used to determine which extant species the fossils have closest affinities with. The age of the fossils and their geographic remoteness from the extant species warrant the establishment of a new species.

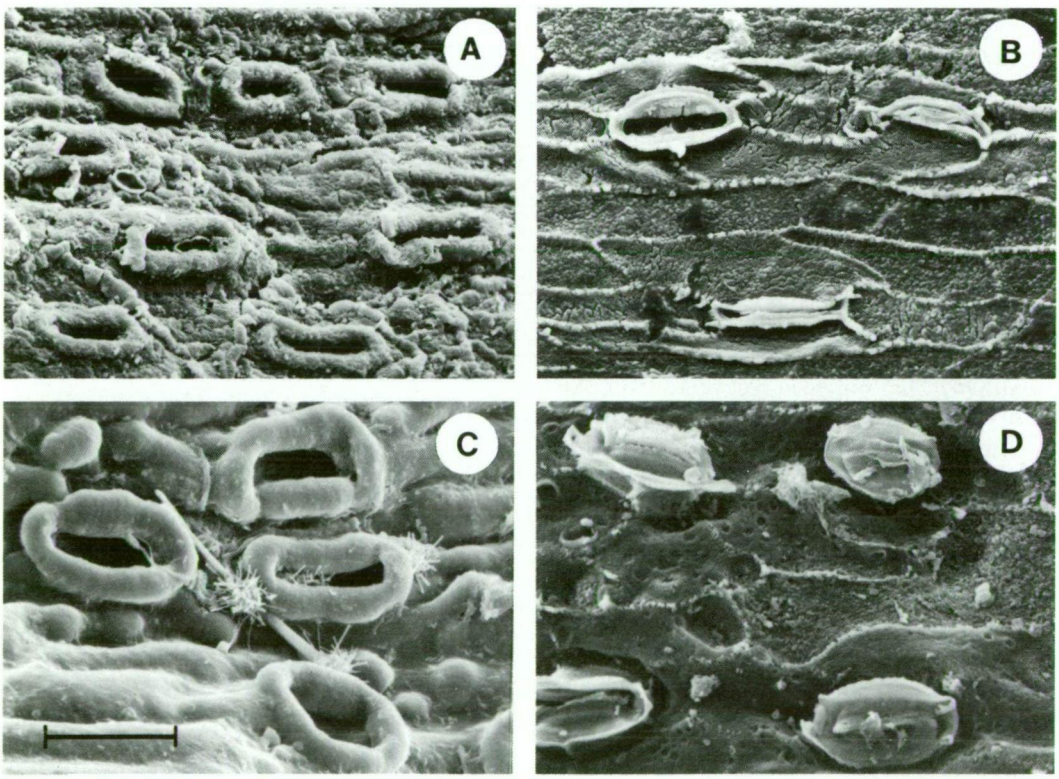

Fig. 6. Scanning electron micrographs of living and fossil *Papuacedrus* species. Scale = 25 μm. A, *P. australis*, outer surface (P-1166). Note the almost unlobed Florin rings and the poor papillae development. B, *P. australis*, inner surface (P-1167). C, *P. arfakensis*, outer surface. Note the almost unlobed Florin rings and the sporadic papillae development. D, *P. torricellensis*, inner surface. This surface was very difficult to clean, and the photograph is the best result from several attempts.

Discussion

None of the three genera to which the fossils were ascribed currently occur in Australia (Fig. 1). *Papuacedrus* occurs as a canopy and subcanopy tree in lower and upper montane rainforest in New Guinea (Grubb & Stevens, 1985). We observed it growing in lower montane rainforests beneath a *Nothofagus* canopy. It is possible that the *Papuacedrus* at Cethana and Pioneer filled a similar niche. *Nothofagus brassii* type pollen dominates both deposits, and at Cethana macrofossils of this type have also been recovered (R. Carpenter, unpublished data). This is the group of *Nothofagus* species which currently occur in New Guinea. Paijmans (1976) considers that *P. papuana* has a wide ecological tolerance and is able to regenerate under dense forest, in the open, and on steep, stony slopes. In many places above about 2400 m in New Guinea the conifer genera *Papuacedrus*, *Podocarpus*, *Dacrydium*, *Dacrycarpus*, *Phyllocladus* and *Araucaria* dominate in the emergent tree layers (Paijmans, 1976; Johns, 1982; Grubb & Stevens, 1985). Most of these genera have been recorded at Cethana (R. Carpenter, unpublished data), suggesting a similar ecological situation.

Little Rapid River sediments also contain a high percentage of *N. brassii* type pollen, and macrofossils of this type are quite common there (Hill, 1987). However, *Papuacedrus* has not been recovered from this deposit. *Libocedrus mesibovii* and *L. jacksonii* may have filled a similar niche to *Papuacedrus*. The three New Caledonian *Libocedrus* species currently occur in the Mt Humboldt region (de Laubenfels, 1972) on the same soil type and in the same area as *Nothofagus*. Little information occurs in the literature regarding the ecology of these forests. *L. plumosa* occurs in the North Island of New Zealand up to 600 m above sea level, and also in the north west of the South Island and *L. bidwillii* occurs mainly in montane and subalpine forests of New Zealand although it is present at low altitudes on the west coast of the South Island (Salmon, 1980). Studies of population dynamics in New Zealand indicate that intermittent disturbance is the principal initiator of *L. bidwillii* regeneration (Veblen & Stewart, 1982; Norton, 1983). These disturbances include infrequent, large scale catastrophic events such as earthquake triggered landslides and/or more frequent, smaller scale, gap forming events. This strategy has also been recorded for *Nothofagus*, especially on suboptimal sites in South America (e.g. Veblen *et al.*, 1980). However, it is difficult to predict the niche of *L. mesibovii* and *L. jacksonii* at Little Rapid River and *L. morrisonii* at Pioneer with any confidence.

The presence of *Austrocedrus* in the Early Miocene of Monpeelyata is of particular ecological interest. The fossil vegetation at Monpeelyata is considered to be cold-adapted (Hill & Gibson, 1986; Hill, 1988), and is dominated by microphyllous angiosperms and podocarps. The extant *A. chilensis* is associated principally with sclerophyllous, arborescent shrubs in the ecotone between forest and the Patagonian steppe on the eastern side of the Andes (Veblen & Schlegel, 1982), although it has also been recorded in association with other conifers and with *Nothofagus* as a sub-canopy species (Veblen & Lorenz, 1987). While it occurs at elevations up to 1000 m it appears to be primarily a low altitude shrub or small tree. *A. tasmanica* has distinctly smaller cones than *A. chilensis*, and this size reduction may be associated with the cooler temperatures at Monpeelyata. However, the presence of *Austrocedrus* at Monpeelyata does not add to the evidence for a cold climate flora, although it is suggestive of open, non-forested vegetation, which is predicted by the large number of species with microphyllous leaves.

None of the fossil species described exhibited any evidence of evolutionary trends among the genera, and on the contrary they offer evidence that the genera *Libocedrus*, *Austrocedrus* and *Papuacedrus* have been distinct since at least the Oligocene. Probably the most interesting feature of the fossils is the information they add regarding the past distribution of the Cupressaceae in the southern hemisphere. The occurrence of *Papuacedrus* in Oligocene forests in Tasmania is not unexpected, since many of the

associated taxa in extant New Guinea high altitude rainforest have been found there (Hill & Macphail, 1983; Hill, 1987; Hill & Bigwood, 1987). The presence of three species of *Libocedrus* in Tasmania in the Oligocene is notable, since the genus is now restricted to New Zealand and New Caledonia and has no previous record outside those geographical areas. Other fossil taxa with closest affinities to extant New Zealand species have been discovered in Tasmania (Hill, 1984, unpublished data; P. M. Wells, pers. comm.), and it is concluded that these taxa must represent conservative lines which were once contemporaneous over wide geographic areas but have since become extinct in Tasmania. The presence of *Austrocedrus* is perhaps the most unexpected, since it no longer occurs in the Australasian region and has not been recorded outside South America. The fossil occurrence suggests that the genus was once much more widespread in the southern hemisphere, but has become restricted during the course of the Tertiary. The presence of these fossils in Tasmania adds weight to Florin's (1963) statement that Australasia was the centre of diversity of the Cupressaceae in the southern hemisphere. The current absence of these genera from Australia is not simple to explain, but may be at least partly due to post Early Tertiary periods of geological stability, when shade-tolerant species were able to outcompete species with a disturbance based ecology.

Acknowledgements

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LEAF LITTER IN TWO SOUTHERN TASMANIAN CREEKS AND ITS RELEVANCE TO PALAEOBOTANY

by R. J. Carpenter and P. Horwitz

(with one table and one text-figure)

CARPENTER, R. J. & HORWITZ, P., 1988 (31:x): Leaf litter in two southern Tasmanian creeks and its relevance to palaeobotany. *Pap. Proc. R. Soc. Tasm.* 122(2): 39–45. ISSN 0080–4703. Botany Department (R.J.C.) and Centre for Environmental Studies (P.H.), University of Tasmania, G.P.O. Box 252C, Hobart, Australia 7001.

Benthic and drifting leaf litter were examined in two parallel creeks in mixed forest in southern Tasmania, and the occurrence of whole leaves recorded. Nothofagus *cunninghamii* leaves were dominant in both the benthic and drift samples, *Atherosperma moschatum* occurred in the drift but only in trace quantities in the benthic samples, *Phyllocladus aspleniifolius* occurred in the benthos but only in trace quantities in the drift samples, and whole *Eucalyptus obliqua* leaves were absent from all samples. Otherwise most species occurred in similar proportions in both creeks and for both sampling strategies. It is concluded that the processes of litter input, leaf buoyancy, and leaf breakdown will result in an unequal potential for fossilisation of the leaves of different species; accordingly, attempts to reconstruct vegetation using macrofossils need to be approached with caution.

Key Words: leaf litter, mixed forest, creek benthos, drift, southern Tasmania, palaeobotany.

INTRODUCTION

Variations in the relative proportions of the leaves of different species represented as leaf litter at surface and benthic levels in lotic and lentic systems, when compared to the surrounding vegetation, may have important implications for both palaeobotanical and limnological research.

Leaves may reach a freshwater system by falling in directly from overhanging vegetation, being blown in (usually from nearby canopy trees) or washed from the litter of the forest floor. The number of whole leaves reaching the water will be dependent upon the amount of litter produced by each species, their size, shape and density, and their susceptibility to mechanical and biological breakdown. Furthermore, buoyancy of the leaves of different species varies so that some may be carried relatively long distances by wind and current whereas others, such as *Eucalyptus coccifera*, fall directly and sink rapidly (Hill & Gibson 1986a). Leaf breakdown may commence with the leaching of water soluble substances followed by invasion of the leaf by micro-organisms, which in turn may be grazed by invertebrates. It is therefore likely that the macrofossil record will be biased towards plants with resistant leaves growing along watercourses. Many of these factors have been discussed by Ferguson (1985) and Birks & Birks (1980).

Little information regarding the input of potential macrofossils into southern hemisphere freshwater systems exists, while even less is known of the feeding ecology of rainforest stream invertebrates (Bunn 1986), and how this may effect the longevity of leaves in the system. The study by Hills & Gibson (1986a) of the distribution of potential macrofossils in Lake Dobson, Tasmania related particularly to subalpine woodland dominated by *Nothofagus cunninghamii* and Epacridaceae/Proteaceae sclerophyll vegetation and not to common Tasmanian cool temperate rainforest elements such as *Atherosperma moschatum* (sassafras), *Eucryphia lucida* (leatherwood) and *Phyllocladus aspleniifolius* (celery-top pine).

Nothofagus leaves with affinity to *N. cunninghamii* and *N. moorei* are abundant in Tasmanian Tertiary deposits (Hill 1983, Hill 1984, Hill & Macphail 1983, Hill & Gibson 1986b) and *Phyllocladus* cladodes have been found in several deposits (Hill & Macphail 1983, 1985). However, other rainforest taxa such as *Atherosperma* (Monimiaceae), *Eucryphia* (Eucryphiaceae), *Anopterus* (Escalloniaceae) and *Aristotelia* (Elaeocarpaceae) have a meagre Tertiary

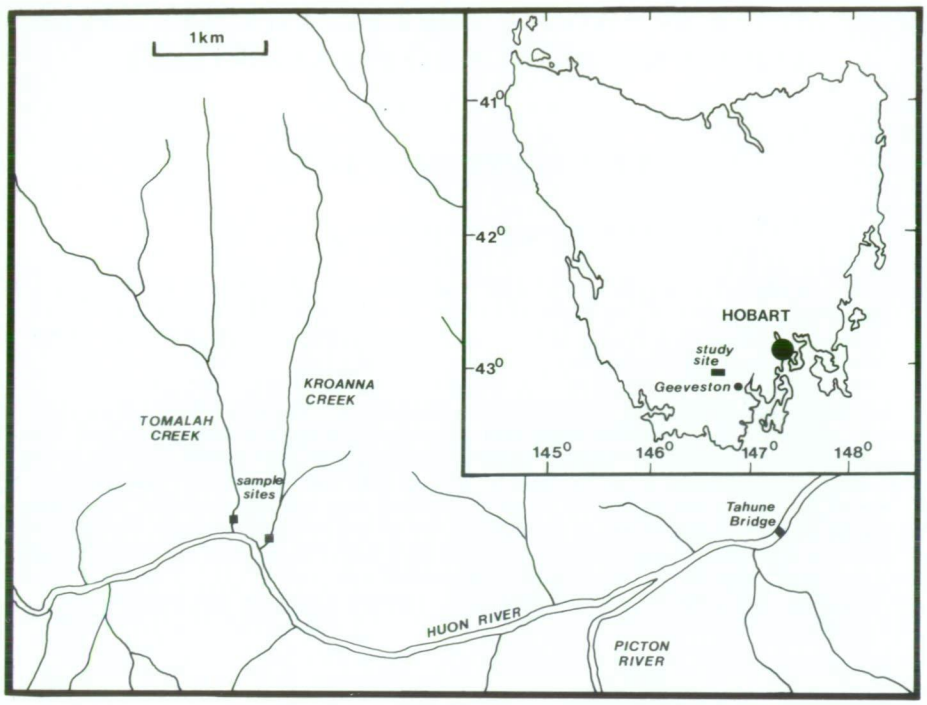

FIG. 1 — The locations of the study sites. For details see Huon 1:100 000 Sheet 8211 (second edition).

macrofossil record despite being considered to have undoubted Gondwanic ancestry (e.g. Raven & Axelrod 1972, Barlow 1981, Jarman & Brown 1983). Tertiary leaves of *Eucryphia* and *Atherosperma* have been documented only from the Regatta Point Plio-Pleistocene deposit (Hill & Macphail 1985). Furthermore, taxa typical of Tasmanian mixed and wet forest such as *Eucalyptus*, *Olearia*, *Phebalium* and *Pomaderris* have no confirmed Tasmanian Tertiary macrofossil record despite being common components of the extant vegetation. A single fossil *Acacia* phyllode is known only from Regatta Point, but is distinct from extant Tasmanian species (Hill & Macphail 1985).

The aim of the present study was to identify the proportionate species composition of whole leaf litter in southern Tasmanian streams which flow through mixed forest, and to determine whether these proportions are altered by using different methods of *in situ* collection. In doing so, we hoped to gain some insights into the potential of leaves of the above taxa to become fossilised, and to relate this information to their relative representation in the Tasmanian fossil record.

METHODS AND MATERIALS

Two permanent streams were selected; Tomalah Creek and Kroanna Creek. Each flows into the Huon River (at approximately 80 m a.s.l.) 4–5 km upstream from Tahune Bridge, near Geeveston, southern Tasmania (fig. 1). Sampling was conducted at sites approximately 30 m upstream of the confluence between each stream and the Huon River. As the streams flow closely parallel to each other, the two sampling sites were no more than 400 m apart. The present study was undertaken during an investigation of drifting invertebrate fauna and the effects of logging activity on this fauna (conducted by the Tasmanian Inland Fisheries Commission).

The streams flow over Permian marine mudstone and the bed loads of the streams consist predominantly of rocks between 0.03 and 0.15 m in diameter.

Kroanna Creek is approximately 0.5–1 m wide at basal flows and at the same levels Tomalah Creek is approximately 1–2 m in width. Whereas the hydrologies of the two streams are essentially similar with respect to temperature regimes, pH,

turbidity and conductivity (R. King, pers. comm. 1987), Kroanna Creek carries approximately half the water of Tomalah Creek.

The composition and abundance of plant species in the surrounding vegetation between the creeks was observed and is best described as mixed forest with eucalypts being the major canopy trees. Wet sclerophyll species such as *Eucalyptus obliqua*, *Pomaderris apetala*, and *Phebalium squameum* dominate the better drained sites with an understorey of plants including *Coprosma quadrifida*, *Cyathodes glauca*, and *Polystichum proliferum*. Rainforest species such as *Nothofagus cunninghamii*, *Eucryphia lucida*, *Anopterus glandulosus* and *Atherosperma moschatum* become more prevalent in the creek gullies. Three *Acacia* species were recorded. *Dicksonia antarctica* was common along both streams.

Two sampling techniques were used in this study; one to examine the benthos and one to examine drift. At each site ten benthic samples were taken using a modified Surber sampler (see Winterbourn 1985); such nets are one of a number of standard techniques for sampling the benthic invertebrates of freshwater systems. For each sample an area of 0.1 m^2 was enclosed and the substratum was manually disturbed to a depth of 50–100 mm. This disturbance throws material such as benthic invertebrates, plant matter (coarse particulate organic matter — CPOM), and substrate into the water column to be carried into the net of 500 µm mesh.

The drift of each creek was sampled by using a drift net, of mesh 500 µm, which enclosed an area of 0.1 m^2. The nets were fixed into place perpendicular to the water flow in riffle sections of the creek and material drifting downstream over a 24–hour period was collected. The nets sampled the entire depth of the creeks. On the 8 and 9 October 1986 four 24-hour drift samples were collected from Tomalah Creek and two 24-hour drift samples from Kroanna Creek. No significant rainfalls had occurred immediately prior to the sampling period (thus sampling was not connected during a spate).

All samples were preserved immediately in 5–10% formaldehyde solution and later stored in 70% alcohol to await sorting. Each sample was then passed through a 2 mm sieve to retain CPOM. Whole leaves, defined as possesing both base and apex, were identified to species level and tallied. The presence of identifiable leaf fragments was recorded as supplementary information. Only whole leaf data were quantified since we consider that whole leaves would be more likely to be identified in palaeobotanical studies. It is therefore to be expected that some bias towards smaller leaves will occur since large leaves will be more susceptible to mechanical fragmentation in the creeks.

RESULTS

All samples were sorted individually (as above) but combined to give both the number and proportion (expressed as a percentage) of each species found in either the benthos or the drift of each creek (table 1). The combination of samples allowed for easier comparisons and analyses and was made possible by the high degree of replicability between each related sample.

With few exceptions (see discussion) the species representation in the litter of the creeks was a good reflection of the nearby vegetation along the creeks.

In general the results from the two creeks were similar. In the benthic samples *Nothofagus cunninghamii* was by far the most commonly occurring species, with an average abundance of 73% in Tomalah Creek and 80% in Kroanna Creek. The major difference between the two creeks was the amount of *Acacia verticillata*; in Kroanna Creek it was the second most common species with 10%, whilst in Tomalah Creek it was found in only trace quantities and *Eucryphia lucida* was subdominant with 19%. *Phyllocladus aspleniifolius* and *Acacia melanoxylon* were present in minor proportions in both creeks. The remaining species occurred only in trace quantities.

In the drift samples *N. cunninghamii* was also the dominant species with 60% in Tomalah Creek and 51% in Kroanna Creek. Similar to the results for benthic samples, drifting whole leaves of *Acacia verticillata* were abundant (33%) in Kroanna Creek but were absent from Tomalah Creek. Trees of this species overhang Kroanna Creek and produce abundant small phyllodes. In Tomalah Creek *Atherosperma moschatum* and *Eucryphia lucida* were present in high proportions in the drift whilst the small leaves of *Coprosma quadrifida* and *Leptospermum lanigerum* were present in low numbers and the six other species were found in only trace quantities. In Kroanna Creek *Atherosperma moschatum*, *Eucryphia lucida*, *Acacia melanoxylon*, *Phebalium squameum* and *Coprosma quadrifida* were present in low numbers and four other species occurred in trace proportions. Frond fragments of the tree fern *Dicksonia antarctica* were common and identified

TABLE 1
Composition of Leaf Litter: the Number* and Percentage for Each Species in Each of the Two Creeks

Species	Benthos		Drift	
	Tomalah	Kroanna	Tomalah	Kroanna
Nothofagus cunninghamii	673 (73)	390 (80)	358 (60)	99 (51)
Eucryphia lucida	174 (19)	17 (4)	83 (14)	9 (5)
Acacia verticillata	1 (trace)	49 (10)	–	64 (32)
Atherosperma moschatum	5 (trace)	4 (trace)	133 (22)	7 (4)
Acacia melanoxylon	43 (5)	12 (2)	1 (trace)	5 (3)
Phyllocladus asplenifolius	17 (2)	10 (2)	1 (trace)	–
Pomaderris apetala	8 (trace)	1 (trace)	3 (trace)	1 (trace)
Phebalium squameum	–	4 (trace)	–	4 (2)
Coprosma quadrifida	–	–	10 (2)	4 (2)
Aristotelia peduncularis	–	–	3 (trace)	–
Prionotes cerinthoides	3 (trace)	–	1 (trace)	–
Monotoca glauca	–	–	1 (trace)	–
Leptospermum lanigerum	2 (trace)	–	8 (1)	1 (trace)
Anopterus glandulosus	–	–	–	1 (trace)
Trochocarpa sp.	–	1 (trace)	–	1 (trace)
Olearia persoonioides	1 (trace)	–	–	–
Totals	927	488	602	196

* Whole leaves only.

in every sample from both creeks. *Acacia dealbata* pinnae were common in Tomalah Creek. Species which were only rarely recorded as large foliage fragments were *Eucalyptus obliqua*, *Olearia argophylla*, *Orites diversifolia*, *Blechnum nudum* and *B. wattsii*. With the exception of *E. obliqua* these species were uncommon in the regional vegetation.

A total of 2213 whole leaves were counted representing 16 species. An additional seven species were found as large leaf, phyllode or frond fragments only (as above), bringing the total to 23 species in the leaf litter of the two streams.

DISCUSSION

The techniques of benthic and drift sampling, usually reserved for the analysis of freshwater invertebrates, have shown some interesting differences between the behaviour of leaves in lotic systems.

Nothofagus cunninghamii leaves were dominant in all samples whereas leaves of the major canopy tree in the area, *Eucalyptus obliqua*, were only recorded as rare, incomplete fragments. *Nothofagus* leaves are small and coriaceous whereas fallen eucalypt leaves are apparently poorly dispersed (Hill & Gibson 1986a) and seem more susceptible to breakdown. Other researchers have also noted a relatively rapid decomposition of eucalypt leaves. For instance, O'Keefe & Lake (1987) found that the consumption of eucalypt leaves by invertebrates began almost as soon as they were placed in a study stream in southern Victoria. The difference in abundance between *Nothofagus* and *Eucalyptus* leaves may also be due to the fact that *N. cunninghamii* trees were relatively more abundant in the moister, shadier creek gullies whereas the eucalypts were usually found in drier locations. Thus in a mixed forest such as this, it can be expected that rainforest species close to the creek are likely to contribute a larger proportion of leaf litter to the creek than *Eucalyptus* spp. and other plants of drier habitats. In order to provide some additional data with which to assess this idea, in May 1987 a transect was constructed perpendicular to each creek, and leaf

litter was collected and tallied from 1 m^2 plots at 5 m intervals up to 25 m. In all over 2500 leaves were tallied. The results were generally as expected. For instance, near Kroanna Creek *N. cunninghamii* leaves decreased from being the most commonly collected neat to the creek until they comprised only 3% of the total leaf litter at 25 m from the creek, whereas *E. obliqua* leaves were low in number and proportion (about 1%) next to the creek and increased to 11% at 25 m. *Atherosperma moschatum* leaves were very common (about 20%) close to the creek but were absent at 25 m. *Eucryphia lucida* and *Pomaderris apetala* leaves were common along transects; the former especially near the creeks, and the latter in drier areas. (The under-representation of *Pomaderris* leaves in the creeks seems to be due to fragility as numerous large leaf fragments were recovered, but comparatively few whole leaves.) Leaves of the shrubs *Anopterus glandulosus*, *Cyathodes glauca* and *Coprosma quadrifida* were very rare in the litter collections, and no phylloclades of *Phyllocladus aspleniifolius* were found.

Two species displayed notable variations in abundance between drift and benthic samples. *Atherosperma moschatum* leaves were mainly in drift samples whereas *Phyllocladus aspleniifolius* was more abundant in benthic samples. These differences probably relate to differences in buoyancy and susceptibility to biological and physical breakdown. Sassafras leaves will readily float and are unlikely to reach the benthos intact. This appears to be principally due to leaching and microbiological breakdown and not due to physical destruction since skeletonised leaves were occasionally recovered as well as leaves in which the mesophyll and epidermis were separating. Broken fragments were rarely recovered. Howard (1973) also noted the rapid breakdown of sassafras leaves relative to those of *Nothofagus cunninghamii*.

The longer leaves remain afloat the less chance they will have of settling out undamaged in anaerobic situations where they could become fossilised. The phylloclades of *Phyllocladus aspleniifolius* are comparatively very thick and leathery and it is quite likely that they would both sink rapidly, and therefore not occur in the drift, and be relatively resistant to mechanical or biological breakdown having reached the benthos. It is probable that the benthic phylloclades have been washed from an unknown distance upstream, since trees were not found close to either creek and no phylloclades were found in the transect litter.

Leaves of other species not recorded as proximal shrubs or trees or in the transect litter were of *Aristotelia peduncularis*, *Prionotes cerinthoides*, *Monotoca glauca*, *Leptospermum lanigerum*, *Olearia persoonioides* and *Trochocarpa* sp. In general these small leaves were found in the drift only and seem to have reached the sampling site from unknown distances upstream.

It is considered that the major results found here, i.e. that *Nothofagus cunninghamii* leaves are dominant in both benthic and drift samples, *Atherosperma moschatum* occurs in the drift but only in trace proportions in the benthos samples and *vice versa* for *Phyllocladus aspleniifolius*, and that whole *Eucalyptus obliqua* leaves were absent from all creek samples, are unlikely to be altered significantly by seasonal variation. Turnbull & Madden (1983) found that the number of basal stems at a site accounted for 64% of the variance in litterfall in southern Tasmanian forests. The remaining amount of variation is unlikely to cause a significant shift in the proportions of leaves of the above species in creeks. For instance a drift sample from Tomalah Creek taken in January 1987 comprised a large quantity of *N. cunninghamii* leaves (62% of all whole leaves found), 8% *Atherosperma moschatum* leaves and did not contain *E. obliqua* leaves (with *Eucryphia lucida* forming the bulk of the remaining leaves). These are very similar results to those found during the observation period in October 1986.

It must be stressed that we do not imply that the sample site is a model of a past situation, or that necessarily it represents a potential fossil site or means of litter conveyance to a fossil site. However, we suggest that the evidence presented here may at least in part be used to explain certain features of the fossil record, including the absence of some taxa which are abundant in extant forests. It is of interest that the benthic data obtained in this report reflect the macrofossil composition of Tasmanian Quaternary sites and the Regatta Point Plio-Pleistocene deposit (Colhoun 1980, Hill & Macphail 1985, R.S. Hill, pers. comm. 1987). These deposits tend to be dominated by *Nothofagus*, with *Eucryphia*, *Phyllocladus* and rare *Atherosperma* and *Acacia* macrofossils.

The results suggest that the processes of leaf buoyancy and breakdown and differential litter input mean that the leaves of *Eucalyptus obliqua* and *Atherosperma moschatum* will fossilise only rarely despite trees of these species being locally common, whereas leaves of *Nothofagus cunninghamii* and *Phyllocladus aspleniifolius* will fossilise readily and abundantly, possibly leading to an overestimation of their actual presence in the

surrounding forest. In this respect Hill & Gibson (1986a) predicted, on the basis of the proportions and distribution of leaves in Lake Dobson, that in the surrounding forest *Eucalyptus coccifera* was rare in relation to *Nothofagus cunninghamii*, whereas in fact the eucalypts are the canopy dominants. No reliable eucalypt macrofossils are known from Tasmania. The paucity of fossil leaves assignable to taxa typical of eucalypt dominated sclerophyll vegetation may also be due to the relatively recent spread of this vegetation type associated with the arrival of humans and frequent fires (Singh, Kershaw & Clark 1981). *Eucryphia* is the only true rainforest plant that is well represented in the litter but has virtually no macrofossil record from the Tertiary. There is therefore some evidence that leatherwood is unlikely to have been common in the Tertiary, at least close to water, a habitat in which it is abundant today. Possibly *Eucryphia* spread during and since the late Tertiary cooling and Quaternary glaciations, which seem to have caused the extinction of numerous species from Tasmania (Hill & Macphail 1985). Leaves of the rainforest shrub *Anopterus glandulosus* appear to be very susceptible to rapid physical and biological breakdown. *Aristotelia* leaves seem to be affected similarly to those of *Atherosperma*. It is predicted that they have little potential for fossilisation. In accordance with the results of O'Keefe & Lake (1987) the thick phyllodes of *A. melanoxylon* appear resistant to breakdown, and should thus fossilise readily. Macrofossils of *Acacia* are known only from Plio-Pleistocene and later sediments (Hill & Macphail 1985) and pollen is first recorded in southeastern Australia in the Miocene (Martin 1978). Therefore, if Acacia occurred in the early Tertiary of Tasmania it must have been very remote from depositional sites.

The results of this report emphasise that in a study of a fossil flora the possibility of the existence of different suites of species away from water must be considered, since leaves of these plants are much less likely to reach a situation where they could become fossilised.

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